THE DEVELOPMENT OF DIATOM-NUTRIENT PALAEOLIMNOLOGICAL INFERENCE MODELS FOR UK LOWLAND RESERVOIRS

by

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A thesis submitted to the University of Plymouth
in partial fulfilment for the degree of

DOCTOR OF PHILOSOPHY

School of Geography
Faculty of Social Science & Business

March 2004

"Don't it always seem to go,
that you don't know what you've got 'til it's gone"

Joni Mitchell - Big Yellow Taxi
From Ladies of the Canyon, 1970, Reprise Records

Abstract

The development of diatom-nutrient palaeolimnological inference models for UK lowland reservoirs

Amy Burgess

Deterioration of UK lowland reservoir water quality through cultural eutrophication is of concern for both water supply and conservation. This study represents the first attempt to develop diatom-based palaeolimnological inference models for the assessment of eutrophication in UK lowland reservoirs. Models are developed from a 46-reservoir calibration set comprising surface sediment diatom assemblages and contemporary environmental data measured seasonally between May 1999 and October 2000. Following removal of outliers the dataset spans a total phosphorus (TP) gradient of 12-242 μgl^{-1} (mean = 63), a chlorophyll-*a* (Chla) gradient of 1.8-25.5 μgl^{-1} (mean = 63) and a conductivity (EC) gradient of 119-781 μScm^{-1} (mean = 424). Reservoir mean annual epilimnetic TP, Chla and EC are reconstructed using weighted averaging (WA) and weighted average partial least squares (WAPLS) techniques. Jack-knifed error statistics for the best performing models (WA inverse deshrinking), are comparable to those reported from similar studies. The plankton provides the dominant habitat for diatom growth in reservoirs, thus plankton-only models are also created and perform almost as well as models developed using all taxa.

Examination of seasonal diatom plankton populations indicates that many taxa display defined seasonal growth preferences. The transition of frustules from live to sedimentary assemblages reveals that reservoir productivity and hence sedimentation rates affect subsequent representation of seasonal diatom populations in surface sediment samples. Fossil diatom assemblages in sediment cores from two contrasting reservoirs are analysed and the UK lowland reservoirs TP, EC and Chla inference models applied to reconstruct reservoir nutrient histories, yielding a fuller account of ecological change than either model alone. Twentieth-century reconstructions from Blackbrook reservoir illustrate an early history of limited impact mesotrophy, followed by a shift to cultural eutrophication during recent decades. Daventry reservoir shows a history of nutrient enrichment to hypertrophy, followed by subsequent re-oligotrophication as a result of pollution-reduction measures. Available historical data support the broad trends inferred by the diatom-based inference models. UK lowland reservoirs are considered suitable environments for the development of diatom-nutrient inference models and their application where intact sediment profiles exist.

Author's Declaration

At no time during the registration for the degree of Doctor of Philosophy has the author been registered for any other University award.

This study was financed with the aid of a studentship from the University of Plymouth and carried out in collaboration with ten regional UK Water Companies.

During the programme of study the work was presented at conferences and seminars and in reports. In addition courses and consultations of relevance to the study were pursued.

Reports:

Eastwood, W.J., Black, S., Burgess, A. and Pearce, N.J.G. (2002) *The palaeolimnological record of recent environmental change at the Daventry Country Park Reservoir, Northamptonshire: A report for Daventry District Council*, Unpublished report, University of Birmingham, UK: 58 pp.

Oral conference presentations:

April 1999	**Postgraduate Palaeoecology Conference**, University of Newcastle.
September 2001	**Freshwater Biological Association (FBA) Annual Meeting**, Royal Holloway (attendance funded by the FBA).

Poster conference presentations:

August 2000	**8th International Paleolimnology Symposium**, Kingston, Ontario, Canada (attendance funded by the University of Plymouth (UoP)).
March 2001	**Bio-monitoring Seminar**, Natural History Museum, London.
July 2001	**Detecting Environmental Change Conference**, UCL, London (attendance funded by the British Ecological Society (BES)).

Additional conferences attended:

October 1998	**British Diatomist's Meeting**, Slapton Sands, Devon.
November 1999	**British Diatomist's Meeting**, How Hill, Norfolk.
November 2003	**CIWEM Water Framework Directive Conference**, SOAS, London (attendance funded by the BES).

Additional courses attended:

December 1998	**BGRG Postgraduate Research Training Course**, Windsor (3 days; attendance funded by the UoP)
July 2000	**Freshwater Algal Course**, run by Drs. Eileen Cox and Elliott Schubert at Kindrogen FSC, Scotland (1 week; attendance part-funded by the British Phycological Society)
February 2001	**Numerical Analysis Course**, run by Prof. H.J.B. Birks at the Environmental Change Research Centre (ECRC), University College London (2 weeks; attendance funded by the UoP)
July 2001	**Water Plants Course**, run by Dr. Sarah Whild at Preston Montford FSC (3 days; attendance funded by the BES)

Further funds obtained:

BGRG Research Fund: £300 towards dating of sediment cores

Signed..AMY...BURGESS.....

Date....OCTOBER..04.....

Acknowledgements

Thanks to my supervisors Neil Roberts, Carl Sayer and Martin Kent for their excellent guidance and continual support and encouragement throughout the duration of my thesis. I am also grateful, to Warren Eastwood for fruitful collaborations on the Daventry project, to Elizabeth Haworth, Carl and Patrick Rioual for discussions enabling successful delineation of troublesome centric diatom taxa, to Helen Bennion for constructive comments on an earlier draft of this thesis and to Dave Twigg for GPS assistance at Blackbrook. Thanks to Liz Hunt, Eric Meyles, Jamie Quinn, John Tibby, Kevin Solman, Neil, Carl, Dan, Mum and Dad for help in the field - your rowing skills, good humour, enthusiasm and efficiency were fantastic and very much appreciated. Many thanks also to friends and family whose generous hospitalities were incredibly welcome after long days in the field.

Ann Kelly, Kevin Solman and Pat Bloomfield provided outstanding assistance in the Lab, both with the provision and preparation of equipment for fieldwork, the development of methodologies for sample collection and analysis and assistance with the operation of laboratory equipment. Pauline Framingham and David Antwis provided first-rate computer support, Roy Moate and Pete Bond expertly assisted with the SEM and Tim Absalom offered valuable advice on all things cartographic. Frank and his team at the University of Plymouth (UoP) Diving and Sailing Centre ably assisted in the development of a Risk Assessment and ensured the provision and maintenance of boats and trailers for fieldwork. I am indebted to the marvellous organisational skills of all technical staff involved and in particular to their unfaltering attention to detail, assuring the smooth running of all fieldwork trips. I would also like to say a huge thank you to the University of Plymouth Security staff. Their good humour, care and support throughout this study have been invaluable, both during sampling trips and whilst on campus working out-of-hours.

The UoP provided financial support to the project as a whole, also enabling attendance at a number of courses and conferences. The British Ecological Society (BES), the Freshwater Biological Association (FBA) and the British Phycological Society (BPS) provided funds facilitating attendance at conferences and participation on additional courses of relevance to the thesis. The British Geomorphological Research Group (BGRG) Research Fund provided financial assistance towards acquisition of core chronologies. I am grateful to all the above for their generous contributions.

This project was carried out in collaboration with ten regional UK Water Companies. I would like to acknowledge their considerable support, including initial permissions to carry out fieldwork and also the provision of chemical and biological data, which was collated by a great many individuals in the regional Water Companies. The logistical support of on-site reservoir staff was considerable and I am indebted to Water Company personnel and independent sailing club, water-ski club and fisheries personnel, both for the provision of boats and for 'hands-on' fieldwork assistance. I am also grateful to all other organisations and individuals, too numerous to mention individually, but whose generous provision of data facilitated my research, making completion of this thesis possible.

Thanks to the many staff and post-grads, both past and present, at the UoP, whose support, encouragement and advice have been forthcoming in so many different ways and without whom completion of this thesis would have been so much more difficult. Thanks also to friends and family who have supported me throughout and who were always willing to lend a hand or an ear. A huge thank you goes to Dan. He is a star and has kept me going during my ups and many downs. Dan's love and understanding have been second-to-none and I certainly wouldn't have completed this thesis without his enduring support. Last, but by no means least, I would like to say a special thank you to Mum and Dad, who have provided constant encouragement and support and were instrumental in fostering my fascination with the natural environment and in 'getting to the bottom of things'. Sadly, Dad did not live to see the completion of my thesis, but I hope he would have been proud.

For Dad

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PART ONE

Introduction & Background

CHAPTER ONE

Introduction to thesis

1.1 Introduction

This study presents the first application of diatom-based palaeolimnological inference model techniques specifically to lowland reservoirs in the United Kingdom (UK). In so doing it enables assessment of the extent of recent environmental change, in particular cultural eutrophication, at these sites, whilst extending the knowledge and application of diatom-based inference models across a broader range of lake typologies.

A large number of diatom-based inference models are currently in existence. These have been developed to reconstruct a wide range of physical and chemical limnological variables (Battarbee *et al.*, 2001). Development of diatom-based inference models follows a simple methodological approach, summarised in Figure 1.1. This approach requires collection of modern surface sediment diatom assemblage data and associated environmental measurements from a suite of sites, together comprising the calibration dataset. Inference models (transfer functions) are then developed for individual environmental variables, essentially comprising estimates of optimal conditions at which each diatom taxon is found in the calibration dataset. Inference models can then be applied to fossil diatom assemblages from sediment cores, thus generating a reconstruction of environmental conditions at the time each fossil assemblage was laid down in the sediment record.

Cultural eutrophication is considered a key issue in relation to freshwater quality (Environment Agency, 1998a). It is the process of nutrient enrichment arising from excessive loadings of phosphate and to a lesser extent nitrate, derived from anthropogenic sources and has long been recognised as a problem in relation to water supply in the UK. In the 1950s, problems with algal blooms blocking filters at water treatment works were experienced (Clegg, 1952). However it wasn't until the 1970s that eutrophication received serious attention (Collingwood, 1977) and it is only recently, in 2003, that legislation has been enacted to tackle the problem effectively. This legislation, namely the recently adopted European Union (EU) Water Framework Directive (WFD) (2000/60/EC), attempts to manage the problem from a catchment perspective, with the aim of returning waterbodies, including artificial reservoirs, to states of minimal anthropogenic impact. Although the WFD takes a multi-proxy approach, diatom-based palaeolimnological inference models for the reconstruction of nutrient histories can help to define and establish effective target

conditions for lake restoration and management, particularly in the absence of long-term monitoring data (cf. Battarbee, 1999; Flower *et al.*, 1997).

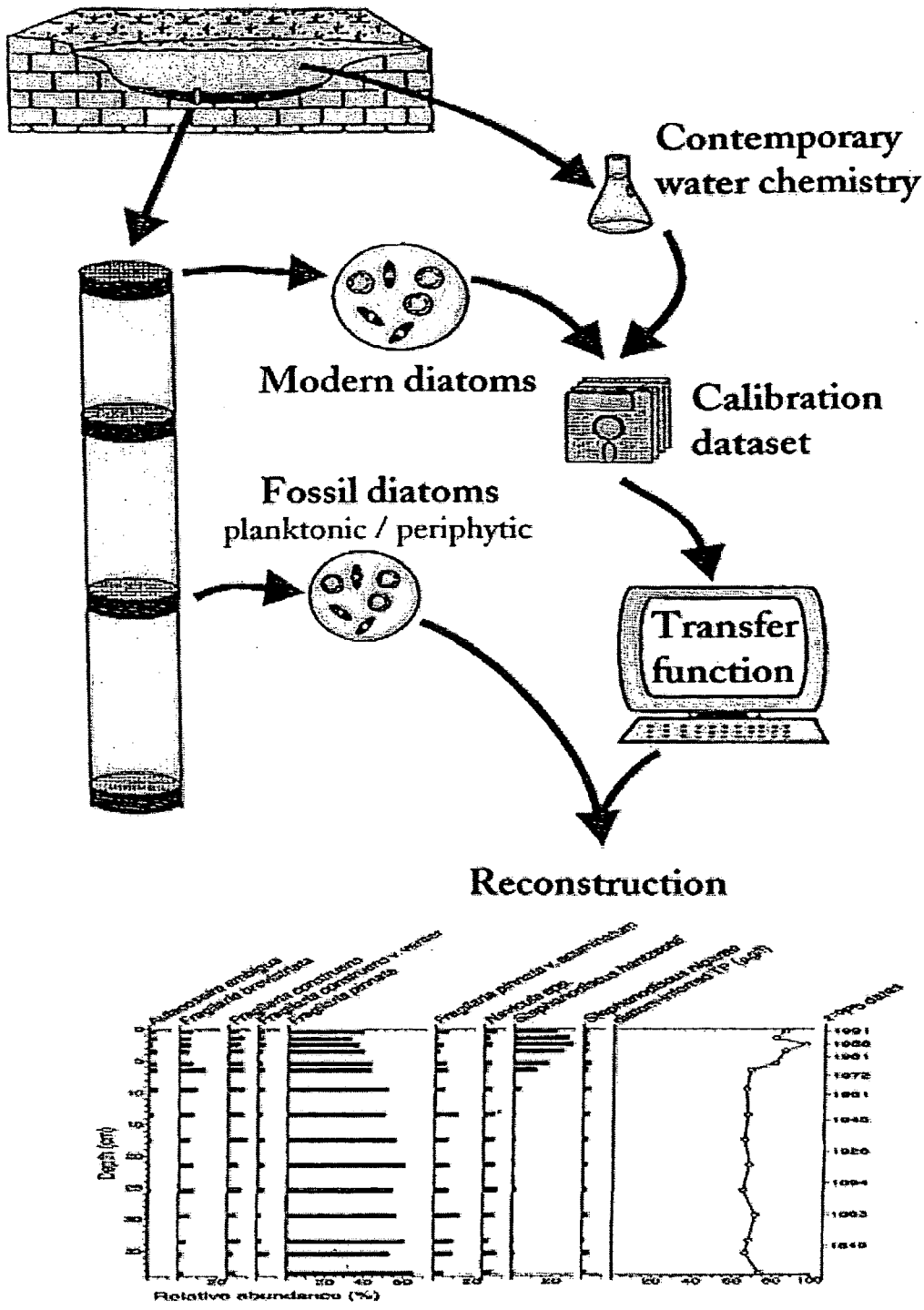


Figure 1.1 **Development of palaeolimnological inference models (modified from Juggins *et al.*, 1995)**

Numerous diatom-based palaeolimnological inference models have been constructed and used to evaluate lake eutrophication and recovery in both individual lakes and across large regions (for a review see Hall & Smol, 1999). The majority of models developed with this aim have been based on total phosphorus (TP) (e.g. Hall & Smol, 1992; Anderson *et al.*, 1993; Fritz *et al.*, 1993b; Anderson & Rippey, 1994; Bennion, 1994; Reavie *et al.*, 1995; Hall & Smol, 1996; Bennion *et al.*, 1996; Lotter *et al.*, 1998; Dixit *et al.*, 1999; Bradshaw & Anderson, 2001; Bradshaw *et al.*, 2002; Kauppila *et al.*, 2002; Tibby, 2004). However models also exist for the reconstruction of other nutrient proxies e.g. chlorophyll-*a* (Brenner *et al.*, 1993; Jones & Juggins, 1995) and total nitrogen (Christie & Smol, 1993; Siver, 1999). More recently the use of habitat-specific inference models have been investigated e.g. Siver (1999), Bradshaw *et al.* (2002) and Philibert & Prairie (2002) developed models based solely on planktonic diatom taxa. The current study is unique in that it provides the first assessment of the potential of European reservoirs for the development of diatom-nutrient palaeolimnological inference models from plankton-dominated assemblages.

Collaborative projects such as the European Diatom Database Initiative (EDDI) (Juggins *et al.*, 2001) have enabled diatom researchers across Europe to make their individual regional calibration datasets and inference models available for fellow palaeolimnologists to apply to fossil diatom data to generate their own environmental reconstructions. The number of diatom-based calibration sets and models is constantly expanding. The harmonisation of species and environmental data across regional calibration sets has enabled the development of large, merged calibration sets and inference models for example the EDDI Combined TP model. Although the inference models developed in the current study are restricted to one particular lake typology, it is envisaged that they will also be applicable across many other deep natural lake environments for the reconstruction of trophic histories.

1.2 Aims

The overall aim of this study is to investigate the potential of UK lowland reservoirs for the development of diatom nutrient palaeolimnological inference models by:

1. creating a calibration dataset for UK lowland reservoirs spanning a broad trophic gradient, comprising mean annual environmental data and surface sediment diatom assemblages.
2. developing diatom-based inference models for the reconstruction of eutrophication histories and comparing the performance of plankton-only models with those based on all taxa.

3. applying these models to down-core changes in sedimentary diatom assemblages for selected reservoirs, and comparing diatom-inferred trajectories with historic records.
4. investigating the seasonality displayed by reservoir planktonic diatom assemblages in response to environmental conditions and exploring relationships between live and fossil diatoms to aid interpretation of sedimentary diatom records.

These aims are to be fulfilled through a combination of modern sampling, the analysis of material from sediment cores and the subsequent application of statistical techniques.

1.3 Artificial lowland reservoirs in the United Kingdom (UK)

The majority of eutrophication inference models constructed to date have been developed from calibration datasets comprising either natural or semi-natural lakes. Where models do exist for artificially created waterbodies, these are based on shallow-lake calibration sets e.g. Bennion (1993, 1994). In contrast to deep waterbodies, shallow lakes provide considerable habitat heterogeneity, which may be more important than epilimnetic conditions in determining diatom species distributions, and consequently diatom-inferred environmental reconstructions can yield spurious results (Bennion *et al.*, 2001; Sayer, 2001). Therefore existing inference models for shallow artificial waterbodies are inappropriate for application to deeper artificial reservoirs.

Although palaeolimnological research has focused on many different types of water body, reservoirs have been relatively little exploited as palaeolimnological archives of recent environmental change. Dixit *et al.* (1999) used a combined calibration set of diatoms in the surface sediments of both natural lakes and artificial reservoirs to assess water quality changes in the northeastern region of the USA. Tibby (2004) successfully developed a DI-TP inference model for southeast Australian water storages. As yet, no inference models have been developed for UK lowland reservoirs. However, these ecosystems are widely distributed in the UK, often possessing well-developed phytoplankton communities. Reservoirs are a significant and economically important source of water supply, particularly in lowland areas of the UK where demand often exceeds the supply available from other sources. Eutrophication in reservoirs has promoted the growth of severe algal blooms, the result of which has been to take such perturbed reservoirs out of supply for both the short (e.g. Cropston and Blackbrook reservoirs, John Smith, STW, pers. comm.) and long term (e.g. Foxcote reservoir, Daldoph, 1999). Therefore it is vital that the functioning of reservoir ecosystems is understood so that the impact of eutrophication can be assessed and recovery programmes successfully implemented in these waterbodies.

Artificial reservoirs are potentially more challenging environments to study than natural lakes, with difficulties primarily relating to their modified hydrological regimes. Seasonally variable inflow and outflow patterns determined by climate and customer demand can dramatically impact upon water levels and affect the balance of habitats for diatom growth. Equipment installed to artificially mix the water column impacts upon the natural process of thermal stratification, which can in turn affect ecosystem functioning and diatom seasonality (Reynolds, 1999). In some poorly designed water management systems, surface sediments can become entrained in the water column, hence disturbing the stratigraphy of the sediment record. Therefore it is important that the specific idiosyncrasies of reservoir environments are understood and accounted for in the process of inference model development from these particular lake typologies.

1.4 Habitat-based inference models

The application of existing artificial waterbody inference models to UK lowland reservoirs may be problematic due to the high level of habitat heterogeneity in the calibration set sites from which these models have been developed. To overcome this problem, habitat-specific inference models may provide a more realistic approach. The water column provides the dominant habitat for diatom growth in deeper waterbodies; therefore diatoms living in this habitat (planktonic diatoms) may provide the most appropriate habitat group from which to develop inference models for UK lowland reservoirs.

An analogous approach was taken by Siver (1999), who described the development of significant inference models based *solely* on planktonic diatoms found in the surface sediments of 50 Connecticut (USA) lakes. His models were able to reliably reconstruct pH, total nitrogen and conductivity, with goodness-of-fit statistics comparable to those recorded in similar studies employing *both* planktonic and periphytic taxa. Based on samples from 29 Danish lakes, Bradshaw *et al.* (2002) developed models for the reconstruction of TP using a) all diatom taxa and b) planktonic taxa only. The plankton-only model performed only slightly less well than the full model, indicating that habitat-based approaches have palaeolimnological potential. The plankton-dominated reservoir calibration set in the current study provides an excellent opportunity to further assess the habitat-based approach.

Plankton-only inference models have the additional advantage that they are based on fewer taxa (see Bradshaw *et al.*, 2002). Because Water Companies have most to gain from protecting and restoring their reservoirs from the effects of eutrophication; it is they who should be most interested in applying these models for the reconstruction of reservoir

nutrient histories. They generally carry out regular sampling and rudimentary identification of reservoir phytoplankton for monitoring purposes. Incorporation of skills in the identification of a restricted range of planktonic diatom taxa (<40 species) could be more easily integrated into these programmes as opposed to developing a working knowledge of the full range of diatom taxa that could potentially be encountered across all habitats (100+ species). With this knowledge, sedimentary diatom sequences could also be examined and the inference models developed in the current study could more easily be applied to reconstruct trophic histories for individual reservoirs.

1.5 Thesis structure

This thesis is divided into four sections. Part One, the introduction and background, introduces the thesis and places it in the context of previously published research. Chapter One provides an introduction to the thesis. Chapter Two presents a review of the literature relevant to this study and is divided into five sub-sections. The first discusses the process of eutrophication, focussing on its importance as an environmental issue in the UK and on the application of the EU Water Framework Directive. The second section introduces diatoms, their occurrence in freshwater environments and the seasonality displayed by planktonic species assemblages. The third outlines palaeolimnological approaches to the study of environmental change and incorporates a discussion of the utilisation of diatom-based techniques for the assessment of eutrophication. The fourth considers recent developments in quantitative palaeolimnological techniques, in particular the use of the inference model approach. The fifth introduces the specific habitat chosen for this study, UK lowland reservoirs, highlighting their main characteristics, the sedimentation processes that occur in these waterbodies and how they have been manipulated to overcome problems relating to excessive algal productivity.

Part Two contains just one chapter, Chapter Three, the methodology. This is divided into three sections: The selection of calibration set and long-coring sites, the field and laboratory methodologies used to collect and process samples and the techniques employed to analyse, interpret and display the resultant data.

Comprising four chapters, Part Three presents the results generated in the current study. Chapter Four summarizes the measured environmental data from the 46-reservoir calibration set. Relationships between variables are investigated and the indirect ordination technique of Principal Components Analysis (PCA) is utilised to detect the major

environmental gradients in the dataset and to identify outlying sites displaying extreme and/or unusual environmental characteristics.

Chapter Five is divided into two sections, comprising an investigation of the full diatom dataset, followed by a similar analysis of the plankton-only dataset. Initially the indirect ordination technique, Detrended Correspondence Analysis (DCA) is employed to investigate patterns of floristic variation in the diatom species data and to identify outlying sites displaying unusual diatom assemblages. Canonical Correspondence Analysis (CCA) methods are then utilised to assess the statistical significance of species-environment relationships. This determines the environmental variables most strongly correlated with species distributions and thus demonstrating potential for the subsequent development of diatom-based inference models.

Chapter Six highlights the importance of understanding temporal variations in diatom species assemblages when utilising diatoms in palaeolimnological research. Data are presented for nine selected reservoirs. DCA and CCA ordinations are used to investigate differences and similarities in diatom species assemblages between sites and seasons. Graphical representations of seasonal environmental data, diatom assemblages and other algal data are presented for each site. Individual DCA ordination diagrams for each site show seasonal shifts and the relationship between 'live' plankton assemblages and 'fossil' surface sediment assemblages. Finally the issue of collecting representative modern surface sediment samples is discussed with reference to examples from three selected reservoirs. Comparisons are made between seasonal planktonic diatom assemblages and those present in different depth surface sediment slices.

Chapter Seven describes the development of diatom-based inference models (transfer functions) from the calibration dataset collected in this study. Inference models are created using the methods of weighted averaging (WA) and weighted averaging partial least squares (WAPLS) regression and calibration. For both the full and plankton-only datasets, three different inference models are generated, for total phosphorus (TP), conductivity (EC) and chlorophyll-*a* (Chla). The performance and predictive ability of the different models are discussed, both in relation to one another and with reference to others published in the literature.

Chapter Eight deals with application of the inference models to fossil assemblages in sediment cores from Blackbrook and Daventry reservoirs in the English Midlands. Diatom-

inferred reconstructions of TP, EC and Chla are generated and trajectories discussed in relation to available historic records. The reconstructive capabilities of the full and plankton-only models are discussed and an alternative inference model, the EDDI combined TP model, is applied to the cores to enable a comparison of diatom-inferred TP trends generated by the different models.

Part Four comprises the discussion and conclusions. Chapter Nine is the main discussion. Since many of the results are discussed as they are presented in Part Three, this chapter considers in detail important overarching issues that have not been debated elsewhere. This embarks on a general discussion of the effectiveness of the inference model approach. Problems associated with the inference model approach are discussed and possible solutions are considered with particular reference to reservoirs. This is followed by examination of the relationships between nutrient concentrations and productivity in UK lowland reservoirs. Finally suggestions for future work are made alongside the conclusions presented in Chapter Ten.

CHAPTER TWO

Diatoms as a palaeolimnological tool in the assessment of reservoir eutrophication

2.1 Introduction

This chapter explores the application of diatom-based palaeolimnological methods for the assessment of trophic state changes in artificial freshwater reservoirs. The process of eutrophication is introduced and its broad impacts on aquatic ecosystems are discussed. The significance of eutrophication as an environmental issue is highlighted with an overview of the political response to its recognition as a problem within the United Kingdom (UK) and European Union (EU). Approaches to the assessment and monitoring of eutrophication trends are considered and models for trophic-state classification are examined. The role of palaeolimnology as a tool in the assessment of eutrophication histories is examined and the importance of diatoms as a palaeolimnological indicator are discussed. Recent advances in quantitative palaeolimnology are reviewed, with particular reference being made to the development of diatom-based inference models (transfer functions) for the reconstruction of trophic state trajectories. Finally, specific issues relating to artificial reservoirs, such as their physical characteristics, the artificial manipulation of such water-bodies, draw-down and sedimentation processes are discussed. Reference is made to the utilisation of such systems in the development of diatom-based inference models.

2.2 Eutrophication

Variations in the chemical composition of natural waters are important in regulating the abundance, composition, and geographical and periodic distribution of phytoplankton. Pearsall (e.g. 1930, 1932) stimulated worldwide research into the link between phytoplankton and water chemistry. Subsequent research has reinforced Pearsall's contention that phosphorus, nitrogen and, in the special case of diatoms, silica are the nutrients whose low natural occurrence in aquatic ecosystems generally makes them limiting. These nutrients are the most important for autotrophic production and are generally scarcer relative to the other 20 or so macronutrients essential for plant growth. Their availability will thus hold primary productivity in check (Reynolds 1984a; Moss, 1996).

Although phosphorus is contained in many minerals, it frequently assumes the role of primary growth-limiting factor in aquatic ecosystems because it readily binds onto clays in soils and hence has a low solubility. Nitrogen is generally considered the next most

important macronutrient. Nitrogen compounds are more soluble than those of phosphorus, therefore nitrate leaches from the soil into watercourses more readily than phosphate and is hence more likely to limit productivity in terrestrial systems (Klapper, 1991). However in some waterbodies e.g. the Shropshire meres, the low availability of nitrogen in relation to phosphorus underpins growth limitation (Moss *et al.*, 1994; James *et al.*, 2003).

An important characteristic of the ecosystem of a static body of water is its *trophic state*, which is characterized by the bio-activity of the photoautotrophic primary producers (Klapper, 1991). The trophic condition of a lake will tend towards equilibrium with its catchment, in which the nutrient supply is balanced by the morphometric characteristics of the basin itself, but one that can be advanced or retarded through time.

'Eutrophic' comes from the Greek for 'fertile.' In its modern meaning the term eutrophic was first used by Weber (1907) when studying the evolution of German peat bogs. Having concluded that the bog contained two distinct strata with different nutrient levels, he labelled the layer rich in nutrients as eutrophic and the one poor in nutrients as oligotrophic (Rodhe, 1969). Consequently ecologists use the term eutrophic to describe biological systems that are nutrient-rich, whilst oligotrophic describes the opposite, nutrient-deficient condition (Reynolds, 1984a). The word '*eutrophication*' literally means "the process of becoming well-fed" (Vollenweider, 1980, p.9). Water bodies experiencing eutrophication are characterised by a rise in primary production caused by natural or anthropogenic enrichment by plant nutrients (Klapper, 1991). Ellis (1989) notes that any enhanced nutrient loading is not balanced by equivalent release through the outflow.

During the last few decades, the word eutrophication has been used more and more in the sense of the artificial and undesirable addition of the plant nutrients nitrogen and phosphorus to waters in the form of nitrates and phosphates (Lund, 1972). The chief sources of human, or 'cultural' enrichment are sewage effluent (largely phosphorus) and agricultural run-off containing artificial fertilisers (predominantly nitrogen). Other contributing sources include stock wastes, aggregations of gulls/wildfowl on open water roosts, some industries and domestic detergents (Brugam, 1978; Moss, 1998a; Moss, 1989; Anderson, 1993; Moss, 1996). In most cases, excessive loading of phosphorus is the primary cause of eutrophication in aquatic ecosystems (OECD, 1982).

2.2.1 The impact of eutrophication on aquatic ecosystems

Eutrophication has proved to be one of the most widespread and serious anthropogenic disturbances to aquatic ecosystems (Lampert & Sommer, 1997) and unpolluted fresh water is one of the most endangered habitats in Britain and north-western Europe (Fitter & Manuel, 1994). All but the most isolated of lowland English lakes have become more fertile through the process of 'cultural' enrichment (Osbourne & Moss, 1977; Pennington, 1978). Eutrophication allows those species that aggressively compete for nutrients to flourish, whilst displacing those with more modest requirements. Thus eutrophication ultimately leads to dominance by a few nutrient-tolerant species and in turn reduces overall biodiversity (Moss, 1996).

In lowland England, cultural eutrophication has received much media attention in recent years, generally being viewed as undesirable, since the process has been accompanied by detrimental changes in aquatic community structure. In shallow, non-stratifying lakes, dense stands of submerged and floating aquatic macrophytes have been replaced with large phytoplankton populations (Osbourne & Moss, 1977; Moss *et al.*, 1979; Sayer, 1997; Sayer & Roberts, 2001). In such cases, reductions in invertebrate and fish diversity as well as loss of plants may have seriously reduced the wildlife and conservation value of these lakes and is of great concern to those responsible for their management (Moss, 1990; Moss *et al.*, 1996; Miskimmin *et al.*, 1995; Haworth *et al.*, 1996; Bennion, 1996).

In deeper stratifying lakes, where submerged macrophytes can only grow in the littoral area, eutrophication usually expresses itself in the form of increased phytoplankton production (Moss, 1990). The larger suspended stocks of phytoplankton lead to a decline in water clarity, with no clear-water phases (Reynolds, 1984; Moss *et al.*, 1996). This not only reduces the amenity and aesthetic value of a lake, but also causes difficulties for water supply companies (e.g. Brierley, 1984, 1985; Hayes & Greene, 1984; Daldorph, 1999).

2.2.2 Models for eutrophication assessment and prediction

Trophic classification

Concern about eutrophication has generally focused attention on nutrient supply as a regulator of lake productivity. Vollenweider's concept of nutrient loading as a factor controlling lake productivity/trophic status has had a major impact on subsequent eutrophication research and lake management. The basic assumption of the concept is that

lake trophic state is dependent either directly on the nutrient supply rate (loading) or, more commonly, on the nutrient concentration in the water (Vollenweider, 1975, 1976).

A trophic classification scheme for freshwaters based on their chemistry was devised by the Organisation for Economic Cooperation and Development (OECD) in 1982 based on the work of Vollenweider (OECD, 1982). This was developed in response to a perceived need to quantify the progression of eutrophication at individual sites. Although other classifications have been developed (e.g. Pearsall, 1930, 1932), the OECD classification is most widely accepted by the scientific community.

Trophic category	Mean P (μgl^{-1})	Mean Chl*a* (μgl^{-1})	Max Chl*a* (μgl^{-1})	Mean SD (m)	Min SD (m)
Ultra-oligotrophic	≤ 4	≤ 1	≤ 2.5	≥ 12	≥ 6
Oligotrophic	≤ 10	≤ 2.5	≤ 8	≥ 6	≤ 3
Mesotrophic	10 – 35	2.5 - 8	8 - 25	6 – 3	3 - 1.5
Eutrophic	35 - 100	8 - 25	25 - 75	3 - 1.5	1.5 - 0.7
Hypertrophic	≥ 100	≥ 25	≥ 75	≤ 1.5	≤ 0.7

Table 2.1 OECD class boundaries for trophic categories (OECD, 1982). Chla = chlorophyll-*a*. SD = Secchi disc depth.

Problems can occur with the OECD (1982) classification however, particularly when the data for sites are inadequate or lacking. The OECD (1982) classification is a 'spatial state scheme' that does not consider changes relative to past conditions, thus it cannot distinguish water bodies having naturally high phosphorus concentrations from those that have such concentrations for anthropogenic reasons. Furthermore it also fails to reveal sites of formerly low nutrient concentrations that have experienced low absolute, but high relative, changes in concentrations that may have endangered their conservation status (Carvalho & Moss, 1995).

Additionally, the availability of nutrients cannot explain all the variation in the primary productivity of the world's lakes and reservoirs, since eutrophication affects every facet of a multivariate aquatic system (Carvalho & Moss, 1995). Carpenter *et al.* (1985) describe the concept of cascading trophic interactions, which can explain differences in productivity among lakes with similar nutrient supplies but contrasting food webs. Although potential productivity at all trophic levels is set by overall nutrient supply, actual productivity depends on the recycling of nutrients, their allocation among populations with different growth rates and upon grazing by zooplankton and invertebrates. Thus, processes that

operate over a wide range of temporal and spatial scales determine the phosphorus availability to phytoplankton. This concept has been key in the recent trend of lake 'biomanipulation' and restoration from eutrophication, particularly in shallow lake systems (e.g. Moss *et al.* 1996).

2.2.3 Eutrophication as an environmental issue in the United Kingdom

The adverse effects of cultural eutrophication have been widely recognised since the 1960s, for example in Australia's Port Phillip Bay (Cullen, 1986) and the American Great Lakes (Beeton, 1966). In the UK, eutrophication was traditionally viewed only as a problem when its symptoms in a drinking-water reservoir could not be treated either mechanically or chemically (Moss, 1998b). For example, Collingwood (1977) concluded that eutrophication was merely an exacerbation of a natural phenomenon. It was not considered to be a problem, since the water industry could implement measures to deal with its consequences. However, such complacency was short-lived. By 1984 the Anglian Water Authority acknowledged that, "the long term influence of eutrophication on the wholesomeness of public supplies from Anglian lowland reservoirs is of concern" (Hayes & Greene, 1984, p.49).

A report by Lund (1980) to the Soap and Detergent Industry Association highlighted the broader impacts of eutrophication in the UK. The report described the adverse consequences of eutrophication, including algal blooms, loss of macrophytes, fish-kills and an overall loss of biodiversity. However, the report used examples drawn largely from two locations; the Norfolk Broads and Lough Neagh. Consequently Lund's findings were misconstrued by politicians in concluding that eutrophication problems were confined to a limited number of sites (Carvalho and Moss, 1995; Wilson *et al.*, 1996).

Sensitivity to the eutrophication problem increased in the UK following the deaths of several sheep and dogs after they drank water containing high concentrations of bloom-forming toxic cyanophytes (blue-green algae) at Rutland Water in the summer of 1989. The legacy of this incident lives on through the numerous warning notices that now appear on the banks of many lowland lakes each summer (Moss, 1996).

In 1990, Lund and Moss updated the first edition of Lund's report (Lund & Moss, 1990). They highlighted the widespread nature of the eutrophication problem in the UK and concluded that the recent problems were anthropogenically and not naturally induced. Successive introduction of water quality legislation signalled the first political

acknowledgement of the eutrophication issue and growing concern of its impacts from the water industry, the general public and conservation bodies.

Prior to 1990 the only legislative potential for protecting against eutrophication of waterbodies was through the system of designation of Sites of Special Scientific Interest (SSSIs) under the Wildlife and Countryside Act 1981. Within the boundaries of an SSSI, steps can be taken to manage and protect the site. However boundaries are generally small and there is no provision for buffer zones to protect waterbodies from catchment land-use inputs. Several subsequent statutes impose duties of consultation on those whose activities may adversely affect SSSIs, however they provide no recourse where consultation is not effective. The same issue of site delineation and lack of buffer zones is true of sites designated under the European Union (EU) Wild Birds Directive (79/409/EEC) and Habitats Directive (92/43/EEC).

Since 1990, water quality legislation has undergone significant development. The Water Resources Act 1991 established the National Rivers Authority (NRA) and introduced a system based on consents required for both abstraction and discharges to English and Welsh waters. The Act introduced the concept of Statutory Water Quality Standards, and the power to designate Nitrate Sensitive Areas and Water Protection Zones. Whilst these concepts appeared laudable their implementation in relation to eutrophication has been criticised. No mention was made of phosphates, derogations were allowed and targets were seen to be easily achievable (Wilson *et al.*, 1996).

In common with Nitrate Sensitive Areas under the Water Resources Act, the Nitrates Directive 1991b (91/676/EEC) makes no reference to phosphates and sets a nitrate limit of 50 mgl^{-1} for designated Nitrate Vulnerable Zones. The 50 mgl^{-1} nitrate limit far exceeds the nitrate concentrations of most eutrophic systems, for example the OECD (1982) preliminary classification of trophic states classifies waters as eutrophic if their mean TN concentrations lie within the range 0.4 to 6.1 mgl^{-1}. The limit therefore appears to be aimed at securing drinking water fit for human consumption as opposed to tackling the issue of eutrophication.

In 1991 the European Urban Waste Water Treatment Directive (1991a) (91/271/EEC) became the first piece of legislation impacting on the UK that was explicitly aimed at limiting phosphate concentrations in addition to those of nitrate. Under the Directive wastewater must be stripped of both phosphates and nitrates. However the requirement only applies to treatment works serving over 10,000 people and discharging into designated

'sensitive' areas. To date only 13 standing waters, 62 rivers / canals and 5 estuaries have been designated as sensitive areas. This equates to just 6.4% of the total river/canal length in England and Wales (Environment Agency, 2002a).

These developments were encouraging, but continued to focus on specific designated sites and the protection of drinking water. They were also often limited to point, rather than diffuse sources of pollution and as such they reinforced the general misconception that eutrophication was not a widespread problem.

An acceptance by government of the widespread nature of eutrophication was slow to emerge. Even during the implementation of the Urban Waste Water Directive the Department of the Environment maintained that freshwater eutrophication was restricted to a few sites (House of Lords, 1991). However studies have shown that around 75-85% of UK standing waters are now eutrophic (Carvalho & Moss, 1995; Palmer & Roy, 2001). In 1998, the Environment Agency (EA) undertook its own far-reaching study and published a report entitled 'The State of the Environment of England and Wales: Fresh Waters' (Environment Agency, 1998a). This report concluded, "about three-quarters of the lakes with SSSI status are affected by nutrient enrichment and many lakes, reservoirs and ponds were suffering from blue-green algae blooms" (Environment Agency, 1998a, p.18). Nutrient enrichment was identified as one of ten priority issues to be addressed if a more sustainable balance between the needs of society and the health of freshwater ecosystems is to be achieved.

Morse *et al.* (1993) estimated that whilst industry produces 8% of phosphate pollution in the UK and human and household waste produces 24%, by far the principal source of phosphate pollution was agriculture (43%). Industrial and human waste tends to result in point source pollution from relatively few factories and treatment works. Thus they are, and to a great extent have been, relatively easily remedied. However the nature of agriculture is diffuse, with phosphate rich fertilisers and livestock faeces being spread over large areas of countryside. The political sensitivities in Europe surrounding farming add to this problem, with vast amounts of Common Agricultural Policy (CAP) funding in essence encouraging maximised yields through the use of artificial fertilisers. To tackle eutrophication a holistic approach to phosphate and nitrate pollution is required, encompassing diffuse as well as point sources of pollution. The impetus to tackle diffuse sources of nutrient pollution has now, it appears, been imposed across the EU by the introduction of the Water Framework Directive (WFD).

2.2.4 The Water Framework Directive (WFD)

Adopted by the European Union (EU) in December 2000, the Water Framework Directive (WFD) (2000/60/EC) states its purpose as the establishment of a framework for the protection of inland surface waters, transitional waters, coastal waters and groundwater. Two of the main aims of the Directive are therefore i) to prevent further deterioration to, and protect and enhance the status of, aquatic ecosystems and ii) to promote sustainable water use (Article 1). Implementation is based on management of water quality at the river basin level. Consequently each river basin in the United Kingdom must be assigned as a river basin district (Article 3) with a river basin management plan drawn up (Article 13). This plan must include measures to prevent or control inputs from diffuse sources liable to cause pollution (Article 11), with substances that contribute to eutrophication (in particular phosphates and nitrates) included in the indicative list of main pollutants (Annex VIII).

The key provisions of relevance to eutrophication are those contained in Article 4, the environmental objectives. The focus of this Article is to ensure the achievement of good status/good ecological potential within 15 years (2015). Annex V of the Directive defines five status classifications, high, good, moderate, poor and bad. In general, high status is defined as a state where there are no, or only very minor, anthropogenic alterations to the biological, chemical and hydromorphological characteristics of the water body. Good status allows for low levels of distortion resulting from human activity but allows only slight deviation from undisturbed conditions. Moderate, poor and bad are defined by ever further distortion from undisturbed conditions (moderate, substantial and severe respectively) and are all below what is acceptable under the Directive.

Article 4 makes a distinction between lakes and artificial / heavily modified waterbodies (including man-made reservoirs), however this distinction is of relatively low importance. Annex V of the Directive defines what constitutes *good status* for natural water bodies and *good ecological potential* for artificial water bodies. Essentially artificial water bodies are treated separately because the demands of restoration to good surface water status would essentially necessitate removal of the 'artificial' element, the dam, without which there would be no reservoir. The requirements for good ecological potential are therefore that the biological, chemical and hydromorphological conditions of the artificial water body are only slightly changed from those associated with the closest comparable surface water body type, given the conditions which result from the artificial characteristics of the water body. The comparable water body type for reservoirs would therefore be lakes. For lakes, biological quality elements include composition and abundance of phytoplankton, other aquatic flora,

benthic invertebrate fauna and fish fauna, whilst physico-chemical quality elements include temperature, oxygen balance, pH, salinity and nutrient concentrations (Moss *et al.*, 2003).

The Environment Agency (EA), the competent body for the implementation of the Directive in England and Wales accept that the separate provision for heavily modified and artificial water bodies is not a derivation and that essentially artificial bodies are to be treated in the same way as their nearest natural comparator (Environment Agency, 2002b; Environment Agency, 2003). Four potential derogations are however possible under Article 4 of the Directive, including; i) where natural conditions or overriding social or economic need prevent the achievement of good status, less stringent objectives may be set and ii) where the failure to achieve good status is for reasons set out in the river basin management plan which are of overriding public interest. These may be of particular relevance to reservoirs, which are generally used for water supply and thus must be assessed in light of their economic and public interest value. Environmental non-governmental organisations (NGOs) see these derogations as broad and ambiguous, with the potential to make the Directive toothless. However NGOs are encouraged by the public nature of the process, with Member States being required to publish their justification for derogations (Cunningham, 2002). Such public justification will leave the decisions of those seeking derogations open to attack from the public and NGO's both through the formal consultation process and if necessary through the courts.

Initial responses to the WFD from the political establishment appear promising. The Environment Agency states that the WFD will be an "important future driver" in the implementation of water policy, (Environment Agency, 2002a, p.30). Meanwhile the Department for the Environment, Food and Rural Affairs (DEFRA) has accepted the realities of tackling diffuse pollution from the agricultural industry and have embarked upon consultation for a strategic review of diffuse water pollution from agriculture that focuses on the need to reduce phosphate and nitrate pollution (Department for the Environment, Food and Rural Affairs, 2003).

The WFD is target-based, aimed at preservation and restoration to good chemical and biological status. Therefore to establish good status the level of distortion resulting from human activity must be assessed and baseline / reference conditions for water bodies must be established so that deviation from 'good status' can be determined. A variety of tools including historical records (e.g. Sayer & Roberts, 2001) and export coefficient modelling techniques (e.g. Reckhow & Simpson, 1980; Rast & Lee, 1983; Johnes & O'Sullivan, 1989;

Johnes *et al.*, 1996) may be important for such an assessment. However, palaeolimnological approaches may provide the greatest potential.

2.3 Palaeolimnological approaches to investigating environmental change

Most lakes have been disturbed to varying degrees, but for an individual lake the timescale of these disturbances is rarely known. There is increasing worldwide recognition of the value of aquatic resources. Governments have become increasingly concerned about the maintenance, enhancement and restoration of aquatic ecosystem integrity. This is highlighted in the EU by the recent adoption of the WFD (Environment Agency, 2002b) and in the USA by The Clean Water Act of 1972 (Barbour *et al.*, 2000). Monitoring programmes must continue for many years before any statistically defensible approaches can detect trends (Dixit *et al.*, 1992). Palaeolimnology can be used expertly as a tool in lake management since it provides a long-term temporal perspective (Anderson, 1995; Birks, 1996). Sedimentary records often provide essential information where historical data do not exist or are of limited quality. Assessment of underlying natural ecosystem variability, definition of pre-pollution baselines and an evaluation of the magnitude, direction and causes of change are all possible using palaeolimnological techniques (Battarbee, 1997). Since practical conservation involves not only effective management but also restoration of ecosystems, palaeolimnology can inform management strategies by helping to define chemical and biological targets for lake restoration (Flower *et al.*, 1997; Battarbee, 1999; Bennion *et al.*, 2004).

Applied palaeolimnology utilises a wide range of biological indicators (proxies) to infer past limnological conditions. Biological indicators that have been utilised include i) algae such as algal pigments (Leavitt & Findlay, 1994), diatoms (Bennion *et al.*, 1996; Kauppila *et al.*, 2002) and chrysophytes (Sandgren, 1991; Cumming *et al.*, 1992), ii) plant remains such as pollen (David *et al.*, 1998; Odgaard, 1999) and plant macrofossils (Birks, 1980; Anderson & Odgaard 1994), iii) zooplankton such as cladocera (Stansfield *et al.*, 1989; Jeppessen *et al.*, 1996), iv) invertebrates remains such as chironomid head capsules (Walker, 1987), v) testate amoebae (Hendon *et al.*, 2001) and vi) fish scales (Davidson *et al.*, 2003). It is now becoming more common for palaeolimnological studies to employ multi-proxy approaches i.e. the use of more than one indicator, to reconstruct ecosystem-level environmental change. Current examples include i) Lotter *et al.* (1998) who used diatoms, chironomids, cladocerans and chrysophyte cysts to reconstruct past environmental conditions in the Alps; ii) Sayer *et al.* (1999) who used diatoms, pollen, chironomids and historic macrophyte records to reconstruct biodiversity changes in a shallow lake ecosystem; and iii) Birks *et al.*

(2000) who made palaeoclimatic inferences based on fossil records of plants (pollen, macrofossils, mosses and diatoms) and animals (chironomids, Cladocera and Coleoptera, Trichoptera and orabatid mites) in the late glacial and early Holocene sediments of Kråkenes Lake, western Norway. Multi-proxy studies provide a greater ecological perspective since they examine the effect of environmental change on organisms at different trophic levels in the food web. These studies have the potential to improve our understanding of the complexities of aquatic ecosystem functioning, particularly when combined with the results of contemporary limnological studies. However, multi-proxy approaches require the collaboration of numerous researchers with different specialist skills and expertise and therefore represent a considerable undertaking. Therefore it is more common for palaeolimnological studies to focus on single biological indicators. Diatoms have to date been the focus of most attention in palaeolimnological research (Battarbee *et al.*, 2001).

2.3.1 Diatoms

Diatoms are unicellular, microscopic (normally between 5-500 μm long), brown-coloured algae belonging to the class *Bacillariophyceae*. Diatom cells consist of two, usually symmetrical valves (frustules) that are held together by belt-like elements called girdle bands. The frustules are composed of opaline silica (glass) and are finely sculptured and ornamented with rows of tiny holes (Dixit *et al.*, 1992; Battarbee *et al.*, 2001).

Diatoms are abundant and widely distributed. They are key components of virtually every habitat where water occurs, both fresh and saline (Stoermer & Smol, 1999). Although there is no accurate estimate of the number of diatom species occurring world-wide, they are an important component of aquatic food chains, fixing a major portion of the Earth's carbon, generating oxygen and supplying high-quality food for animals (Dixit *et al.*, 1992).

2.3.2 Importance of diatoms for palaeolimnological research

Ideally, biological indicators should (according to Dixit *et al.*, 1992) be, i) simple; ii) able to quantify the rate of degradation (or recovery) in water quality; iii) applicable over large geographic regions; and iv) furnish data on background or 'reference' conditions and natural variability. Diatoms satisfy these criteria more fully than any other aquatic organism (Hall & Smol, 1999; Battarbee *et al.*, 2001).

After death the resistant siliceous frustules of diatoms preserve well in sediments under most conditions. They are taxonomically diagnostic, permitting identification to species or sub-species level, thus providing a record of the diatom flora at the time the sediments were laid

down. In addition, diatom remains represent the organism itself, which has been directly influenced by ambient environmental conditions during its lifetime. This is in contrast to biological indicators such as pollen, which are representative only of a reproductive stage. Particular species of diatoms are characteristic of different habitats within a lake, i) planktonic diatoms live within the water column; ii) tychoplanktonic (or meroplanktonic) taxa live interchangeably both in the water column and on the sediments (Battarbee *et al.*, 2001); iii) epiphytic diatoms grow attached to plants; iv) epipelic (often termed benthic), diatom species live on sediments; v) epilithic diatoms grow attached to rocks; and vi) epipsammic diatoms live on sand grains. Diatoms that grow on a substrate, i.e. epiphyton, epipelon, epilithon and epipsammon, are collectively termed, periphyton (Round, 1981a). Examination of assemblages of diatoms preserved in lake sediments can therefore directly reflect the balance of these different habitats and the relative productivity of lake diatom communities over time. This can indirectly reflect lake water quality and habitat structure (Lotter *et al.*, 1998; Sayer, 2001).

Diatom species can have narrow optima and tolerances for many environmental variables, for example pH, alkalinity, nutrient concentrations and salinity. Diatoms can also respond quickly to changes in their surrounding habitat because they can disperse and replicate rapidly (Dixit *et al.*, 1992). This ecological sensitivity makes them extremely powerful tools with which to explore and interpret many ecological and practical problems, particularly in relation to environmental change (Stoermer & Smol, 1999; Battarbee *et al.*, 2001). Diatom-based palaeolimnological inference models were initially developed for the reconstruction of pH (e.g. Birks *et al.*, 1990). Subsequently models have been developed for the reconstruction of lake trophic status based on the relationship of diatom species to phosphorus, nitrogen and chlorophyll-*a* concentrations (e.g. Hall & Smol, 1992).

2.3.3 Diatom ecology

Phytoplankton have been shown to have both seasonal and trophic preferences across different lake types. Diatoms are just one group of algae encompassed by the term 'phytoplankton'. As a group, their main growth regulating factors are turbulence, light climate, temperature, nutrients (silicon, phosphorus and nitrogen) and biotic interactions (Patrick, 1948, 1977; Lund, 1950). As a group they are known to be particularly good competitors during periods of turbulence, low light and comparatively low temperatures and moderate nutrient availability (Hutchinson, 1967; Willén, 1991; Reynolds & Irish, 2000). However, large species-specific variation occurs that is dependent upon the relative balance of growth regulating factors (Willén, 1991; Reynolds & Irish, 2000).

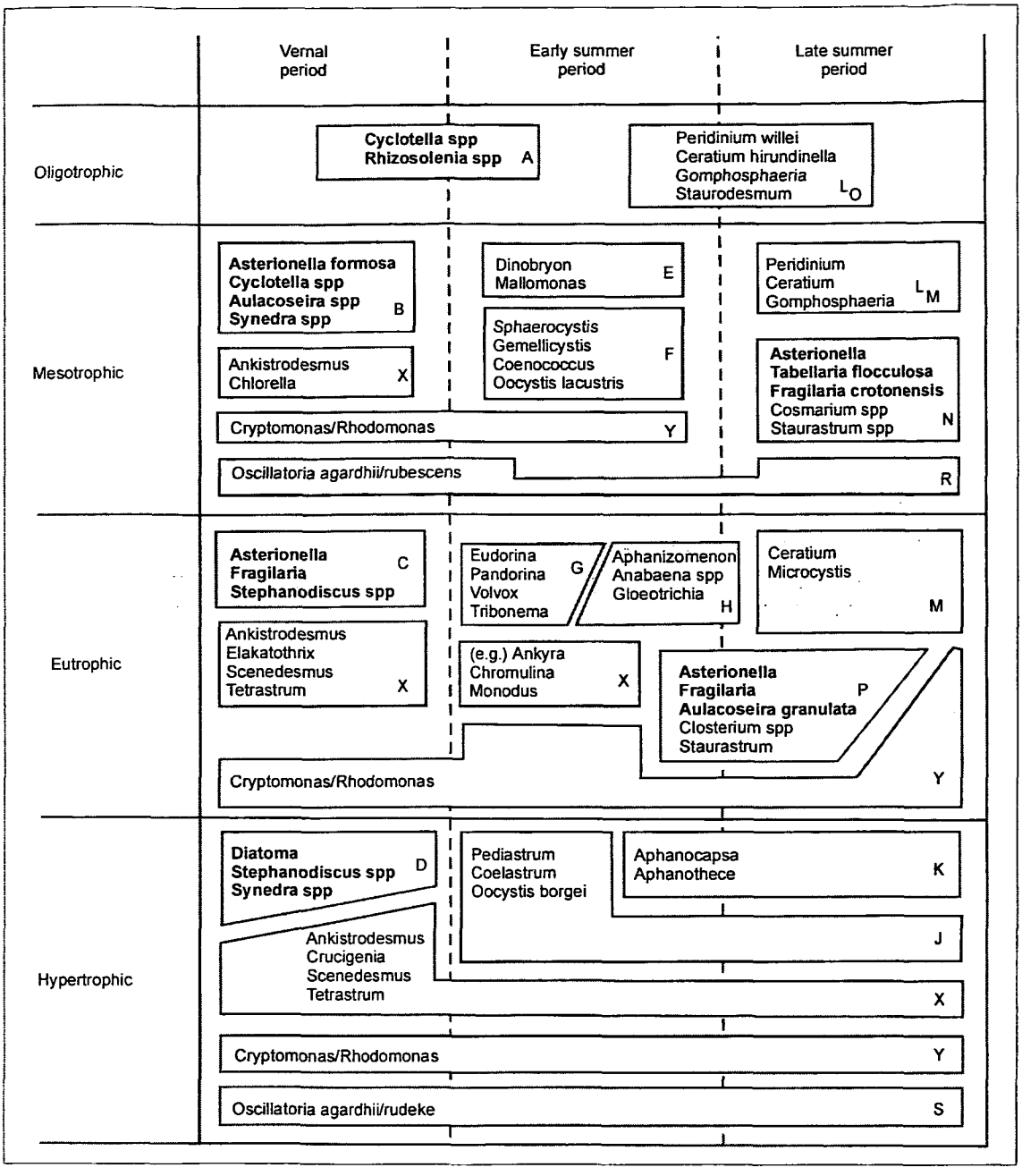


Figure 2.1 **Assemblages of temperate phytoplankton (A-S, X, Y) and some representative species, one or more of which may grow well, relatively well or become abundant in the types of lakes during the approximate seasons of the year indicated (Reynolds, 1984b). Diatoms in bold.**

The occurrence, abundance and periodicities of different diatom taxa are illustrated in Figure 2.1. This diagram displays the 24 different phytoplankton species assemblages of Reynolds (1984b), a broad classification that attempts to characterise the phytoplankton seasonal periodicities amongst temperate lakes of differing trophic status. In varying lake types within each trophic category, differing seasonal sequences of the assemblages shown have been observed and are discussed in detail by Reynolds (1984b). The generalised sequence in many eutrophic lakes follows the seasonal trend, C → E/G → H → L/M, with to varying extents, returns through P, X or Y (Reynolds, 1984b). The diatom species

represented by this sequence include a vernal bloom of *Asterionella formosa*, *Fragilaria* spp. and *Stephanodiscus* spp., sometimes followed by an autumnal bloom of *A. formosa*, *Fragilaria* spp. and *Aulacoseira granulata*. Between these periods, chlorophytes, cyanophytes chryptomonas and rhodophytes usually dominate the phytoplankton assemblage. In mesotrophic lakes such as Lake Windermere, the generalised sequence is B $\rightarrow$ E/F $\rightarrow$ N/L_M. In these lakes, diatoms dominate in the vernal period, represented from among, *A. formosa*, *Cyclotella* spp., *Aulacoseira italica / islandica* and *Synedra* spp. The re-establishment of diatom-dominated assemblages may occur at the onset of overturn in the autumn. Diatom species typical of this period include *Tabellaria flocculosa*, *Fragilaria crotonensis*, *A. granulata* and *A. formosa*.

Just as it is true for natural lakes, temperate artificial reservoirs are subject to significant seasonal variability. Reynolds (1999) observed that the selective mechanisms of phytoplankton in reservoirs are no different from those operative in lakes, however he noted; "the selective outcomes are substantially influenced by the environmental conditions which pertain in natural and artificially-constructed basins" (pp.439-440). In deep, pump-storage, well-mixed lowland reservoirs, the generally observed phytoplankton sequence is C $\rightarrow$ H/S $\rightarrow$ P (i.e. diatoms, cyanophytes, diatoms). However, in reservoirs that become stratified during the summer, X, G, F, E, R or Y assemblages may occur during the period of stratification i.e. the phytoplankton is dominated by chlorophytes, *Oscillatoria* spp., chrysophytes, cryptomonas and/or rhodomonas during this period (Reynolds, 1999).

Within these generalised seasonal species assemblages, there is further variation. The seasonal availability and limitation of different nutrients and silica creates competition between diatoms, with different species able to tolerate different environmental conditions. For example, Kilham (1971) reported a successional sequence from dominance by *Melosira* (now termed *Aulacoseira*) to *Asterionella* to *Tabellaria* to *Stephanodiscus* as dissolved silica concentrations declined. Further, Tilman *et al.* (1982) related these observed changes to the combined influence of both silica and phosphorus (Figure 2.2), therefore they described the sequence in relation in terms of seasonal changes in the ratio of Si:P. With declining Si:P ratios they predicted a seasonal succession from *Synedra* to *Asterionella* to *Fragilaria* to *Diatoma* to *Stephanodiscus* and *Cyclotella meneghiniana*.

Low N:P ratios indicate nitrogen limitation (Gilford & Hecky, 2000). Smith (1983) analysed growing season data from 17 lakes throughout the world and observed that low nitrogen to

phosphorus ratios (N:P) favoured dominance by cyanophytes, whereas they were rare when N:P exceeded 29:1 by weight.

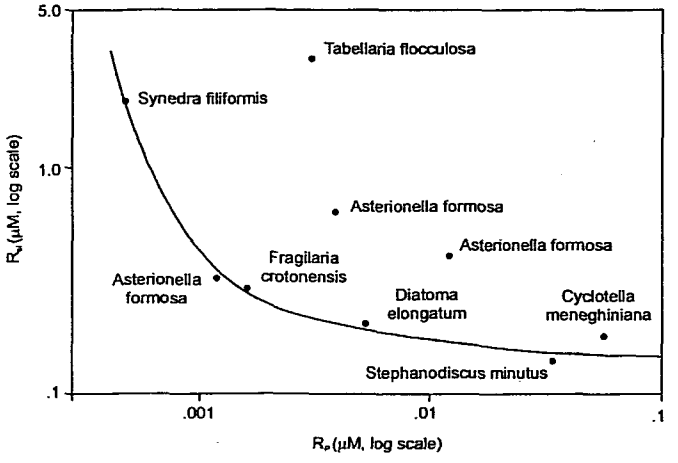


Figure 2.2 Curve illustrating interspecific tradeoffs in the competitive abilities of freshwater planktonic diatoms in laboratory conditions at 20 °C. Phosphorus is on the 'x' axis and silica is on the 'y' axis (Tilman *et al.*, 1982).

Seasonal variation can create conditions favouring domination by either *r*- or *K*-strategists. Species defined as *r*-strategists have a fast growth rate but often respond to the onset of nutrient-limitation by undergoing lifecycle changes at the population level by producing resting stages (Kilham & Kilham, 1980). *K*-strategists are slower growing but are able to adapt to low resource availability through physiological adaptation of individual cells. Seasonal periodicity generally begins in the spring, with efficient light-harvesting, low temperature tolerant, *r*-selected species (e.g. the diatoms *A formosa* and *Aulacoseira* spp.), taking advantage of a turbulent water column enriched with nutrients by winter recharge. As available nutrient concentrations decrease, *K*-selected species (e.g. *Stephanodiscus astraea* and cyanophytes) begin to dominate due to their more efficient use of available resources and hence superior competitive ability under conditions of low resource availability (Turpin, 1988).

The seasonal growth preferences of planktonic diatom species can have a profound effect on the relative representation of different species within surface sediment diatom assemblages taken in different seasons. Sayer (1997) theorised the effect of timing on the representation of different diatom taxa in surface sediment samples (Figure 2.3). He suggested that, if contemporary diatom data were compared with surface sediment samples taken in different seasons, recently sedimented species would be best represented. Sayer (2001) observed this phenomenon in practice. He suggested that the greater representation of recently deposited

diatoms resulted because they had experienced a reduced period of decomposition / dissolution. Thus, contemporary monitoring of phytoplankton populations can facilitate determination of phases of diatom production and hence sedimentation. This can in turn assist in the selection of the most appropriate time for the collection of surface sediment samples, so that samples are not differentially biased towards particular species with different seasonal preferences. So that the two main periods of diatom growth are represented and that summer dissolution processes had affected sedimentary diatom assemblages in a similar way, late winter sampling was recommended by Sayer (2001). However, Tibby (2004) sampled surface sediments throughout the year. When a constrained canonical correspondence analysis was performed, with day of the year as the sole variable, sampling date did not explain a significant amount of variance in the diatom data.

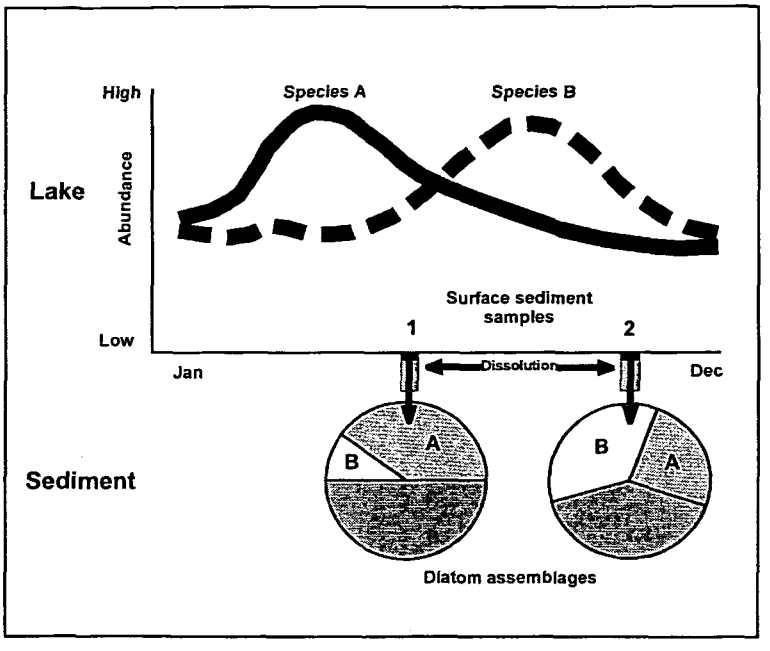


Figure 2.3 The theoretical effects of the timing of surface sediment sampling on the representation in the sediments of species with different seasonal requirements (after Sayer, 1997, 2001)

2.3.4 Taphonomic issues

Environmental reconstructions are limited by the quality of the original data from which they are derived. A fundamental pre-requisite in palaeolimnology is that the fossil remains found in the sediment record accurately reflect the composition of living communities present at the time of their death (Roberts, 1998). However, transformation of modern diatom communities into the fossil record is controlled by a complex array of often site-specific taphonomic processes that operate both in the water column and in sediments, promoting spatial and temporal mixing, dissolution and breakage (Flower, 1993).

Diatom remains preserved in sediments are assumed to be representative of the floristic composition of communities present in a lake at a given point in time. Thus in theory the surface sediment assemblage should integrate diatom species from the full range of available lake habitats.

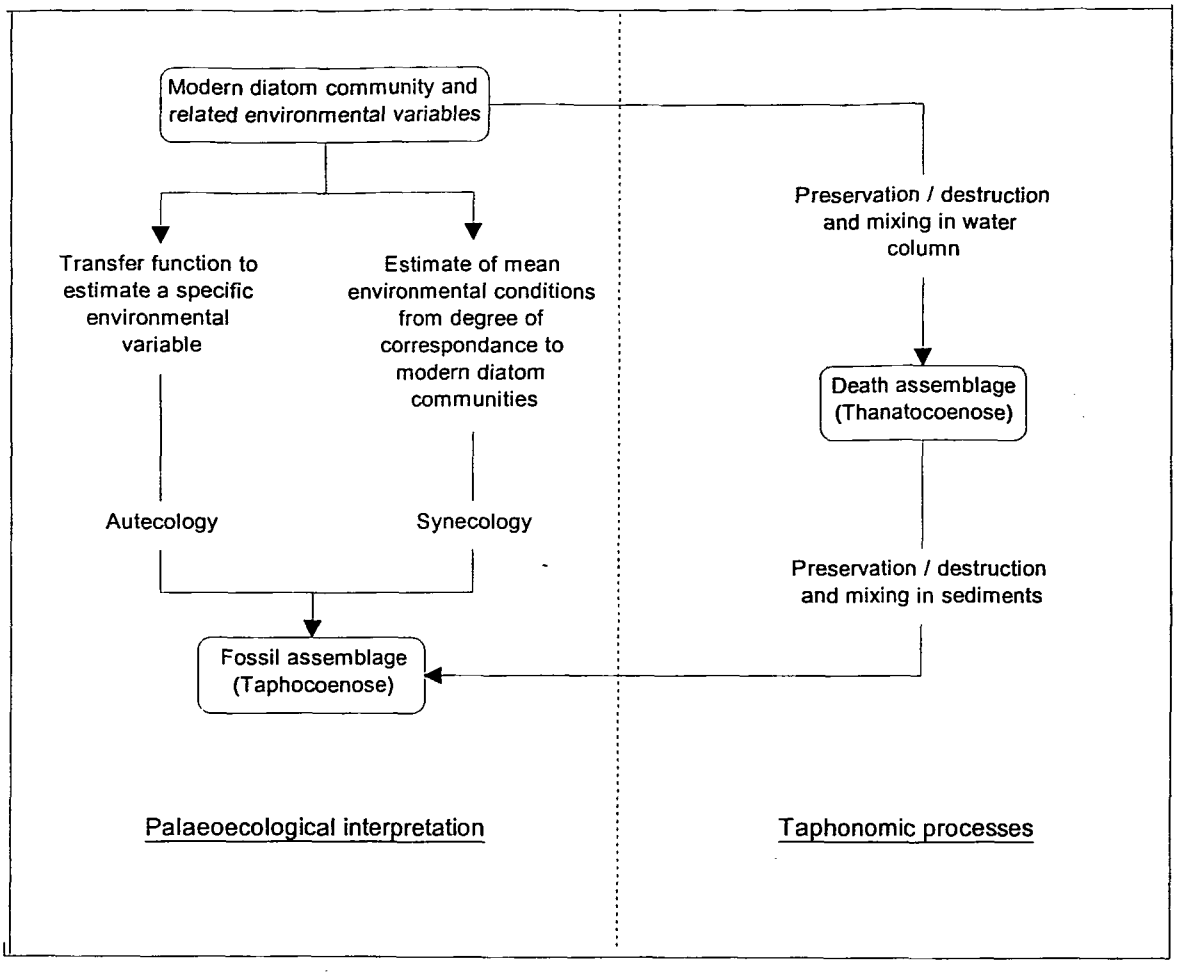


Figure 2.4 Theoretical relationship between diatom taphonomy and palaeoecology (Gasse, 1988; Barker, 1992).

Where microfossils are poorly preserved, problems may arise, both through taxonomic uncertainty and more subtly from the alteration of the death assemblage as a result of the differential robustness of species (Barker *et al.*, 1994; Ryves, 1995; Sayer, 2001). Based on a consideration of a variety of lakes, Flower (1993) has observed that diatom preservation declines with increasing pH, temperature, coarseness of sediment, grazing and bioturbation, water depth and exposure. Preservation generally increases with diatom robustness, diatom and sediment accumulation rate and diatom concentration. Understanding and predicting diatom preservation in lake sediments is a complex multivariate problem of fundamental importance to palaeoecology and diatom-based palaeoenvironmental reconstructions (Figure 2.4).

The precise taxonomy of diatoms in living communities and in fossil assemblages is essential to any palaeoenvironmental interpretations based on fossil diatom assemblages (Barker *et al.*, 1990). Diatom dissolution and thus the taxonomic resolution that is possible, much limits the reliability of interpretations that can be drawn from examination of sedimentary diatom records. For example, Fritz (1990) reported that in shallow calcareous and saline lakes, diatoms may be entirely absent and both concentrations and preservation quality decrease down a core. Parker & Edgington (1976) reported that deep freshwater lakes with low sediment accumulation rates and high pH promoted dissolution and breakage in both the water column and sediment.

Flower (1993) concluded that the first few decades following deposition are the most important in conferring diatom resistance to dissolution. Preservation generally increases with diatom robustness. Therefore diatoms dissolve preferentially (Flower, 1993). Thus it is of concern for interpretation of sedimentary records that any small, lightly silicified diatom species will be under-represented in the sediment record relative to those which have robust, highly silicified frustules resistant to dissolution. The gross valve surface area to volume ratio (SA:V) was found to be a useful first-order approximation of a particular diatom species' propensity to dissolve by Barker *et al.* (1994). These authors reported that species with the lowest SA:V ratios, such as *Stephanodiscus neoastraea,* are those that are best preserved, whereas *Stephanodiscus parvus*, which has a SA:V ratio almost an order of magnitude greater than *S. neoastraea*, were less well preserved.

Where suspected groundwater movements occur, diatom dissolution can be extensive, since groundwater discharge continually reduces the silicate concentration in the interstitial waters (Anderson, 1990c). Bioturbation at the sediment surface also exacerbates dissolution by enhancing breakage and fracturing of diatom frustules, which may increase dissolution (Flower, 1993).

Grazing by zooplankton and other invertebrates may also influence the resultant fossil diatom assemblages. For example, colonial forms such as small *Fragilaria* spp. are more resistant to grazing than unicells. Thus, if a lake's sedimentary diatom assemblage is strongly influenced by grazing, then there may be under-representation of certain palatable diatoms (Anderson, 1990c). In addition, the action of mollusc grazing on epiphyton will result in selective grazing of more easily removed, stalked diatoms (e.g. *Gomphonema* spp.) as opposed to grazer-resistant, adnate taxa such as *Cocconeis placentula* (Underwood & Thomas, 1990; Jones *et al.*, 2000).

2.4 Developments in quantitative diatom-based palaeolimnological methods

Prior to the 1980s, most diatom-based palaeolimnological assessments of trophic state changes were based on the ecological interpretation of qualitative shifts in the abundance of individual diatom species in sediment cores (e.g. Bradbury, 1975; Osbourne & Moss, 1977; Battarbee, 1978). Early attempts to quantify trophic state changes from sedimentary diatom assemblages were based on a number of semi-quantitative productivity indices, for example the ratio of planktonic centrales to planktonic pennales (the C:P ratio of Nygaard, 1949) and the ratio of planktonic araphid to centric diatom taxa (the A:C ratio of Stockner & Benson, 1967 and Stockner, 1971). However most of these indices were considered oversimplistic (Battarbee, 1986; Hall & Smol, 1999), with researchers often reporting contradictory trends (e.g. Brugam, 1979). "The ecological requirements of diatoms do not strictly follow frustule morphology.... [and] too much ecological information is lost by clumping diatoms into just two categories" (Hall & Smol, 1999, p.136).

Despite the usefulness of semi-qualitative assessments of past water quality, ecosystem managers often demand assessments of aquatic ecosystem dynamics that enable them to determine baseline or 'natural' levels of key parameters and to quantify ecosystem changes accurately. For this requirement to be fulfilled, more quantitative palaeolimnological approaches were developed. Initial attempts to make interpretation more objective centred on the use of multiple linear regression models to 'classify' sedimentary diatom taxa into ecological categories based on species-environment information available in the literature (e.g. the DITI model of Agbeti & Dickman, 1989), or according to contemporary distributions of diatom species in surface sediment calibration lakes (e.g. the TROPH1 model of Whitmore, 1989). However these methods had a number of shortcomings (see Hall & Smol, 1999 for a discussion), including the assumption that diatom species respond linearly to environmental gradients (ter Braak & van Dam, 1989).

Since the mid 1980s, diatom-based palaeolimnology has become more quantitative and objective (in statistical terms) in its approach (Anderson, 1995a). Multivariate statistical techniques have been used to relate diatom distributions to environmental gradients and to develop diatom-based inference models for the quantitative reconstruction of environmental conditions (Fritz *et al.* 1993b; Anderson, 1995a; Bennion, 1994; Siver, 1999; Bradshaw *et al.*, 2002; Philibert & Prairie, 2002a). Such diatom-based inference models (transfer functions) are derived from a calibration (training) set of modern surface-sediment diatom assemblages and contemporary environmental data from a large number (typically 30+) of individual lakes (Battarbee *et al.*, 2001). Several models have been proposed, but weighted

averaging (WA) and weighted averaging partial least squares (WAPLS) have been the most suitable for the development of quantitative inference models (Birks, 1998). The initial development and application of these inference models in palaeolimnology were associated with lake acidification and pH reconstructions (ter Braak & van Dam, 1989; Birks *et al.* 1990). This was primarily because of the well-known relationship between diatoms and pH. Similar methods have now been applied to a number of other parameters, including trace metals (Dixit *et al.*, 1991), salinity (Fritz *et al.*, 1991; Gasse *et al.*, 1995; Ryves *et al.*, 2002), and nutrients (Hall & Smol, 1992; Anderson *et al.*, 1993; Reavie *et al.*, 1995; Bennion *et al.*, 1996; Lotter *et al.*, 1998; Kauppila *et al.*, 2002; Tibby, 2004).

Diatom calibration datasets and inference models are becoming increasingly large and comprehensive (e.g. Bennion *et al.*, 1996). Although this may provide more reliable estimates of species optima and distributions (Battarbee, 1999), application of these models relies upon rigorous validation and on an understanding of the strengths and weaknesses of the approach. This should include consideration of the various methods employed and a sound ecological appreciation of the environments in which models are applied (Fritz *et al.*, 1993b; Anderson & Odgaard, 1994; Bennion, 1994; Anderson, 1995; Anderson, 1997; Birks, 1998; Sayer, 2001).

Weighted averaging regression and calibration

Weighted averaging (WA) regression and calibration was developed by ter Braak (1987). It is a two-step procedure incorporating both regression and calibration. In the regression step, the responses of taxa to the contemporary environment are modelled. In the calibration step, the environmental variable of interest is predicted from the fossil assemblage. WA has advantages over earlier linear-based quantitative techniques because it is based on both the concept of niche-space partitioning and on the ecologically plausible assumption that organisms respond unimodally to environmental gradients. It has also been shown to perform well with noisy, species-rich, compositional data with many zero values (Birks, 1998). In addition, it avoids the loss of ecological information, because each taxon is assigned an optimum and tolerance value (ter Braak & van Dam, 1989; Birks *et al.*, 1990).

Figure 2.5 illustrates the basis of the weighted averaging (WA) method. Along an environmental continuum, a taxon's optimum is defined at the point where it is most abundant. The value of a taxon's optimum can be established by taking an average of all values where the taxon occurs, weighted by the relative abundance of the taxon at each site (ter Braak & van Dam, 1989). The inferred optima are then used to calculate the value of the

variable for sedimentary records by taking the average optima of all taxa occurring in the sediment, again, weighted according to abundance. The degree of tolerance can be built into the calibration so that species with narrow tolerances are given greater weighting (Birks, 1995).

Despite their widespread use, WA approaches are reported to suffer from two major limitations. Firstly, they are sensitive to the distribution of the chemical variables in the calibration set. The method performs well only when calibration set samples have a reasonably even distribution along the chemical gradient and when species are sampled over their entire range (ter Braak & Looman, 1986). Secondly, they disregard unexplained variance since they assume that species assemblage composition is influenced by the single modelled environmental variable (ter Braak & Juggins, 1993). Acknowledgment of these limitations has seen the recent development and improvement of WA techniques.

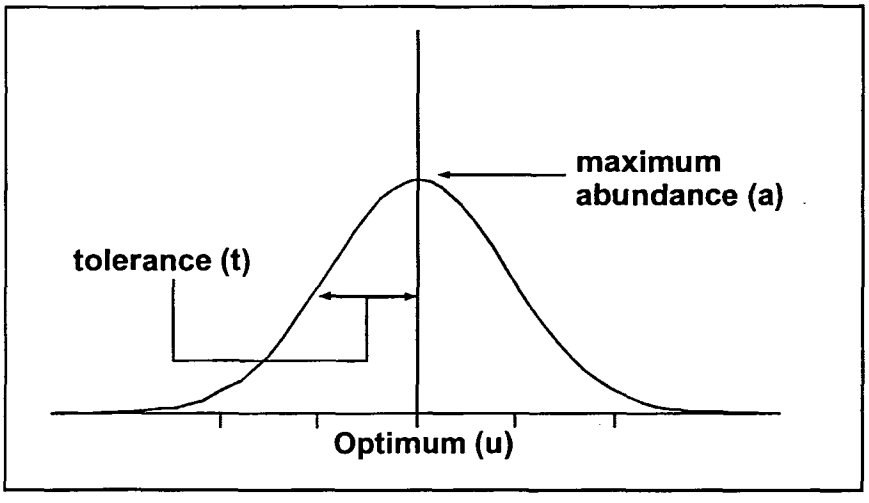


Figure 2.5 Gaussian response curve (modified from ter Braak & Looman 1986).

Weighted-averaging partial least squares (WAPLS)

In reality the composition and abundance of biological assemblages are influenced by multiple environmental factors. The incorporation of linear partial least squares (PLS) regression into WA regression (ter Braak & Juggins, 1993) can overcome some of the weaknesses associated with WA regression alone. The resultant technique, weighted averaging partial least squares (WAPLS), considers residual correlations in the biological data in an attempt to improve estimation of taxon optimas, and in turn improve the inference model's predictive ability (Birks, 1995; Bennion *et al.*, 1996). However, in common with WA techniques, WAPLS is sensitive to the distribution of the environmental variable in the calibration dataset. Techniques such as WAPLS perform best with data exhibiting low

'noise'. In data simulations, ter Braak & Juggins (1993) showed that WAPLS could give a 70% reduction in prediction error in datasets with low noise. Therefore it is desirable to minimise 'noise' wherever possible, particularly through careful design of sampling procedures for calibration sets along the primary environmental gradients of interest.

WAPLS shows a large improvement if secondary environmental gradients i.e. structured noise, exist (Birks, 1995). The aim of WAPLS is to select the 'minimal adequate model', whereby "the model should be as simple as possible and should contain no redundant parameters or components" (Birks, 1998, p.312). This is dependent upon the intended application of the model for reconstruction purposes and may often involve a compromise between a model with the lowest prediction error using several components and a simpler model (fewer components) but with a lower maximum bias.

The most powerful means of model validation is to compare directly the reconstructions derived from the models against historical environmental records e.g. Bennion *et al.* (1995), Marchetto & Bettinetti (1995) and Bradshaw & Anderson (2001). However, in the absence of long-term monitoring data the optimal models are often considered to be those that give the lowest root mean squared error of prediction (RMSEP) (Birks, 1998).

Other approaches

There are a number of other techniques for modelling species-environment responses that have not yet been fully explored, but which may improve further the calibration techniques currently available in palaeolimnology. In recent years, a modern analogue technique (MAT) has been more frequently employed by palaeolimnologists. MAT involves finding the closest modern analogues for a fossil assemblage and taking a weighted average of the modern environment of those closest analogues. Lotter *et al.* (1998) found that there were only small differences in RMSEP between MAT and WAPLS, but that the maximum bias under MAT was larger. MAT has shown potential in lake conservation and restoration programmes by identifying modern lakes as possible analogues for what the lake of interest might once have been like (Flower *et al.*, 1997; Simpson, 2003).

WA and WAPLS modelling methods assume unimodal responses of all diatom species to environmental gradients. Artificial Neural Networks (ANNs) are dynamic computer systems that are able to learn the relations between input and output data and have the ability to model and incorporate taxa with a mixture of responses (Birks, 1998). This is ecologically relevant because in reality species responses may be highly variable and include a

combination of linear, unimodal and skewed distributions. Although ANNs are seldom used in ecology, Racca *et al.* (2001) report that the combined approach of WAPLS and ANNs produced more statistically robust models than using each model individually. This indicates that future improvements in the predictive ability of diatom-based inference models may be possible using combined modelling approaches.

A further approach showing potential is that of Bayesian statistics. This approach uses probability distributions throughout the inference as opposed to the point estimates used in WA and WAPLS methods (Vasko *et al.*, 2000; Toivonen *et al.*, 2001). Birks (1998) suggests that Bayesian approaches may be of greatest potential where species-environment relationships are relatively weak.

Another potential development is to use modern regression techniques (generalised linear modelling and generalised additive modelling) to explore the extensive data on species-environment relationships that are contained in calibration datasets more fully. Šmilauer & Birks (1995) provide a detailed discussion of these approaches.

2.4.1 Problems associated with diatom-based inference models

A major concern with any microfossil-based WA model is that of its robustness - in terms of its applicability at different sites, its precision and its accuracy. Fritz *et al.* (1993b), Anderson (1995a), Anderson (1997) and Sayer (2001) highlight a number of errors associated with the development and application of diatom-based inference models. These errors are the result of uncertainties in, i) temporal and spatial variability of water chemistry and surface sediment samples calibration set data ii) subsequent problems of taxonomic resolution and suitable modern analogues, iii) accurately estimating species optima, iv) diatom ecology.

Temporal and spatial variability of the calibration set species and environment data

The quality of output from a model is a direct function of input data quality. Bennion & Smith (2000) suggest that good estimates of annual mean environmental data may improve diatom-based inference models. Despite the recent methodological developments in statistical calibration, Birks (1995, 1998) considers that the current key limitation in quantitative palaeoenvironmental reconstructions is the need for high-quality modern calibration sets, combining consistent and detailed taxonomy with comparable methodology and sedimentary environments, and a sufficient contemporary gradient of the environmental variable in question.

Although the ordination techniques used in the majority of quantitative reconstructions are statistically well-founded, and the output may well suggest strong correlations between the distribution of biological remains and a particular environmental variable, it must be remembered that many environmental variables are highly inter-correlated, and to a large extent may simply be proxies for the same thing. Thus in many cases it may not be possible to unravel a single variable driving limnological change (Fritz *et al.*, 1993b). Factors controlling diatom abundance in most lakes are multivariate and stochastic intra- and inter-annual variability in environmental conditions is experienced. These cannot be fully accounted for in models where a single measure of the variable is to be predicted (Fritz *et al.*, 1993b).

Taxonomic resolution, harmonisation and 'no analogues'

More recently, data sets from different regional calibration sets have been amalgamated through international co-operation. Bennion *et al.* (1996) created a diatom-based total phosphorus (TP) inference model based on data from 152 lakes in northwest Europe and Stevenson *et al.* (1991) developed the Surface Waters Acidification Project (SWAP) calibration set based on data from 170 lakes covering southern Norway, southern Sweden and upland Britain. The European Diatom Database (EDDI) (Juggins *et al.*, 2001) presents an amalgamation of data from across Europe, where regional calibration sets are combined and harmonised thereby expanding chemical and biological ranges and in turn improving the predictive ability and general applicability of previously published regional inference models. Although this decreases the chance of experiencing problems with 'no-analogues', issues arise concerning data harmonisation between the different datasets.

Species optima and ecological considerations

Derived optima are relative to the calibration dataset environmental gradient length. Bennion *et al.* (1996) report that a longer environmental gradient length reduced the problem of truncated species distributions frequently observed in small calibration sets. More importantly, there is generally a poor understanding of the environmental factors governing past and present diatom distributions. WA and WAPLS modelling approaches are based on percentage relative abundance species data. Since species abundance is partly a function of competitive advantage, the derived optimum for an individual taxon will be relative to the other species present in the calibration dataset (Birks, 1995). The limitations of any 'black-box' statistical modelling approach, are that the ecology of individual taxa is ignored (Bennion, 1994; Sayer, 2001; Bradshaw *et al.*, 2002).

2.4.2 Habitat-based inference models

A shortfall of current diatom-inferred models is that they are created using only surface sediment species assemblages. An advantage of using this resource is that it theoretically constitutes an amalgamation of diatoms and other material from all habitats in the ecosystem which have accumulated over the last year or so. However, every lake is different, for example in terms of its bathymetry, or the presence/absence of aquatic plants. These differences are known to occur irrespective of nutrient concentrations, particularly in shallow lakes which can exist in 'alternative stable states' (Carpenter *et al.*, 1985; Moss *et al.*, 1996).

At present, only limited research has been undertaken to determine the relative influences of each habitat in individual lakes of the calibration set. One such recent example has been the development of diatom-inferred pH (DI-pH), total nitrogen (DI-TN) and conductivity (DI-EC) inference models based solely on planktonic diatoms in the surface sediments of fifty Connecticut lakes by Siver (1999). In conclusion, Siver argued that a comparison of goodness-of-fit statistics for models using only planktonic taxa, only periphytic taxa, and all taxa would provide the most appropriate means to evaluate effectively the use of each habitat group in constructing inference models. Bradshaw *et al.* (2002) adopted such an approach when they developed and compared the performance of DI-TP inference models based on all taxa and planktonic taxa only, from the surface sediments of 29 shallow Danish lakes. They concluded that the performance of the model based on all taxa was superior, but that of the plankton-only model was only slightly inferior. The similarity in performance was thought to be due to the domination of planktonic diatom taxa in the surface sediments of the calibration set sites.

The ecological approach to the creation of inference models can be extended further to focus on each individual habitat (plankton / epiphyton / epipelon). Species optima can be defined using samples of living diatoms (e.g. Gasse *et al.*, 1997) and further, separate transfer functions can be created for each habitat group based on modern samples (Sayer, pers. comm.). However, Sayer (2001) suggests that in shallow lake environments in particular, diatom-based inference models should not be used in isolation to infer past environmental conditions.

2.5 Reservoirs

Human dependence on water is as true today as in prehistoric times, and the area served by water sources has been extended with pumps and pipes, as well as by the creation of new artificial storage lakes - reservoirs (Taub, 1984). The Romans pioneered the use of reservoirs for water supply and the concept of a reservoir dam was one of their great legacies. However, following the decline of the Roman Empire, little use was made of reservoirs for public water supply until their revival during the last hundred years, in parallel with the growth in population and energy consumption (Henderson-Sellers, 1979). Consequently, most reservoirs are extremely young, only a few decades old (Morris & Fan, 1998).

Surface reservoirs are the means most often used for collecting and storing excess water, which is then released at times of the year when demand exceeds the supply. The storage of water in reservoirs is crucial in most water supply systems around the world, not only for direct human and animal consumption, but also for irrigation, industrial processing and hydro-electric power (Henderson-Sellers, 1979). Two basic types of storage reservoir can be built: an *impounding* reservoir and a *pumped storage* reservoir.

Impounding reservoirs are created by damming a stream / river so that the water upstream of the dam collects in a lake behind the dam. This is a good solution if the volume of water in the inflow(s) is sufficient to fill the lake fairly quickly e.g. upland areas subject to high annual rainfall - most early dams and reservoirs were constructed in areas such as these (Patrick & Stevenson, 1988). However more recently, new reservoirs have been sited in the wider, flatter lowland valleys where the flow of the incumbent stream(s) is often too low to fill the reservoir within an acceptable time. In these cases, the natural inflow is replaced or supplemented by an artificial pumped inflow. The water to achieve this is usually abstracted from a nearby large river, often in a different catchment area, when it is in spate and pumped to the reservoir overland for storage; hence the term *pumped storage* (Henderson-Sellers, 1979).

2.5.1 Lowland reservoirs and eutrophication

All reservoirs, as barriers to natural drainage, rapidly accumulate silt, inorganic nutrients and organic matter; and thus are especially susceptible to eutrophication accelerated by high sedimentation rates and nutrient enrichment (Kimmel & Lind, 1972). Lowland reservoirs are often closer to the centres of demand but they often hold water of lower quality, since they generally contain water from downstream locations, where pollution levels may be higher.

Nutrient loads may be sufficient for eutrophication of the water to occur and in addition, low water quality necessitates the need for complex and costly purification methods before the water becomes potable (Henderson-Sellers, 1979). A number of lowland reservoirs have experienced such problematic and regular algal blooms that, despite the application of remedial measures, it has been necessary to take them out of permanent supply e.g. Foxcote, Buckinghamshire (Daldorph, 1999). Other reservoirs can spend substantial periods out of public supply when their water is rendered untreatable due to the proliferation of filter-clogging and toxic cyanophyte blooms e.g. Cropston (John Smith, STW, pers. comm.).

2.5.2 Reservoir characteristics

Just as slightly different combinations of key factors such as geology, topography, climate and human activity influence the physical and chemical characteristics of individual natural lakes, the same is true of artificial reservoirs. Characteristics of natural and artificial waterbodies may be similar if they occupy similar climatic zones and have comparable hydromorphological characteristics (Morris & Fan, 1998). Both lakes and reservoirs are populated by many of the same species, because life that can exist in aquatic environments is largely dependent on similar generic controls, including light penetration, mixing depth, availability of oxygen, temperature, nutrient availability and hydraulic retention time (Henderson-Sellers, 1979).

Chemical composition

The introduction of chemicals into a lake depends on the chemistry of precipitation and materials within the drainage basin. These are highly variable from one body of water to another. The bedrock underlying a lake basin and its catchment largely determines the chemical composition of ground water and usually controls the relative abundance of ions in the aquatic environment (Taub, 1984). The major cations found in lakes are calcium, magnesium, sodium and potassium, since their salts tend to be the most soluble and are readily leached. The major anions are carbonate, bicarbonate, nitrate, chloride and sulphate, with phosphate occurring in often low but significant concentrations for aquatic plant productivity (Taub, 1984).

Light availability

Net photosynthesis is theoretically possible within the layer of water called the 'euphotic zone' and, as a rule of thumb, the euphotic depth (deepest extent of the euphotic zone) for phytoplankton is that at which about 1% of the surface light still remains (~2.4 times secchi depth). It lies higher in the water column, at ~5% of surface light, for bulkier aquatic plants,

whose respiratory needs per unit weight are higher than those of microscopic algae (Moss, 1998a). The euphotic zone will vary seasonally and spatially as a result of turbid inflows and variations in algal populations (Morris & Fan, 1998).

According to the concept of the euphotic depth, lakes can be divided into littoral (edge) and pelagic (open water) zones. The littoral is that part of the lake where the euphotic zone extends to the bottom, so that net photosynthesis by either algae or larger plants is possible on the bottom. The pelagic zone is the remainder of the lake, where the bottom lies below the euphotic zone and whose communities are dependent on the import of organic matter from the overlying water or the littoral (Moss, 1998a). The shape of a lake basin exerts a major influence on its biology, since this affects the balance between open water and littoral communities. In general, lakes that are shallow or shallowly sloping and have a high proportion of shoreline to the total area of water tend to be the most productive (Whitton, 1979).

Light penetration in reservoirs may be limited by high turbidity from suspended solids delivered by the river or pumped inflow, or from the re-suspension of bottom sediment by wave action (Tibby, 2000, 2004). Water transparency will vary seasonally and spatially as a result of turbid inflows and variations in algal population dynamics. During seasonal run-off events, the inflow of turbid water may reduce the euphotic zone to a fraction of a metre in depth (Morris & Fan, 1998). The lacustrine zone with clearer water and lower sediment loads generally occurs closer to the dam wall and this may exhibit characteristics more similar to natural lakes (Morris & Fan, 1998).

Temperature stratification

Water bodies more than a few metres deep have a strong tendency to divide (stratify) into layers, which may not readily mix because of changes in water density caused by differences in temperature (Moss, 1998a; Morris & Fan, 1998). Lake stratification (Figure 2.6) is largely driven by the seasonal variation in solar energy and layers of warm and cold water are a striking feature of larger lakes in summer. The sun warms the surface water, forming a warmer, lighter, well-oxygenated layer called the *epilimnion*, which, because water decreases in density with temperature above approximately 3.94 °C, floats on the colder, darker, oxygen-depleted water of the *hypolimnion*. The upper layer, the epilimnion, and lower layer, the hypolimnion, are separated by the *metalimnion* - a narrow transitional zone where a temperature gradient, the *thermocline*, of as much or more than 1 °C m^{-1} may be detected (Moss, 1998a). In British lakes the thermocline is often at a depth of about 9-10

m (Fitter & Manuel, 1994). Its existence is of paramount importance in determining water quality, presenting a physical barrier between the two layers, severely inhibiting vertical downward mixing of momentum, heat and dissolved oxygen. Without regular renewal of its supply of oxygen, the ability of the hypolimnion to support life diminishes during the period when the thermocline prevails. Anaerobic conditions arise and the water becomes of little use (Henderson-Sellers, 1979).

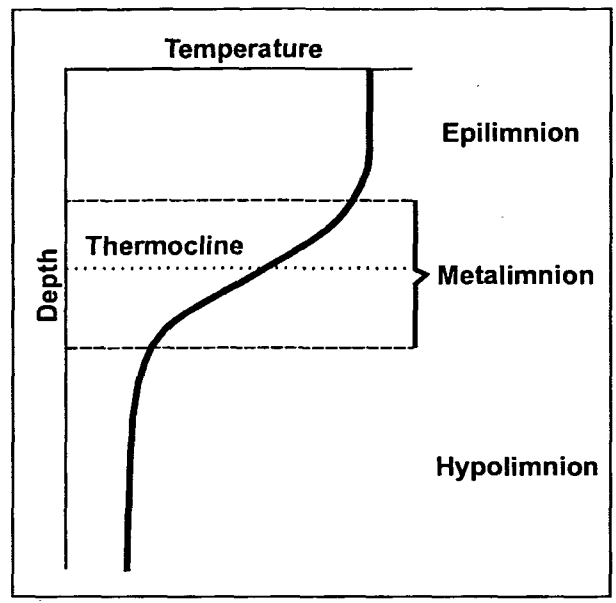


Figure 2.6 Typical summer temperature profile in a stratified reservoir (Lampert & Sommer, 1997)

Lakes that form a thermocline earlier in the year undergo a reverse change, known as the *overturn*. The epilimnion cools and then starts to sink. Wind currents mix the entire water column vertically, breaking down the thermal stratification until the lake becomes isothermal. This is an important event in the annual cycle of stratifying lakes, since sediments, nutrients and organisms near the bottom are stirred into the water column. Nutrients that have accumulated in the deeper water are also returned to the surface, where they can promote algal growth in the spring as temperatures rise, ice cover disappears and daylight hours lengthen (Morris & Fan, 1998).

Wind is the primary factor causing vertical circulation in lakes and higher winds will cause deeper circulation and increase the depth of the epilimnion. The thermal structure of a lake can also be subject to significant temporal and spatial differences as a result of varying wind direction and velocity. Winds of sufficient strength, duration and fetch will overcome temperature-induced stratification and completely mix the water column (Morris & Fan, 1998).

2.5.3 Lake and reservoir development

Figure 2.7 illustrates the graphical model of Deevey (1984), showing trophic equilibrium and its displacements. The space within the cylinder represents time and trophic status. Lakes are described as undergoing an early sigmoidal ontogeny. This represents changes during the stabilisation of the newly formed waterbody. A long-lasting but irregular trophic equilibrium follows, where the ecosystem is stable and there are no external factors causing change. Subsequently, displacements can cause a shift in trophic state from the natural equilibrium, A, to a new state, B. Upward displacement is eutrophication, while decreases in trophic state are shown as a downward displacement. Only upward displacements are of relevance to the current study and are provided by cultural eutrophication. The departure to a new resilient equilibrium is maintained unless there is a change in the driving stress, but this is reversible on reduction of the driving stress. Beyond space B, lies another tubular region, C, in which stability is unidirectional and collapse of the system is certain. This could happen if eutrophication were to continue or worsen.

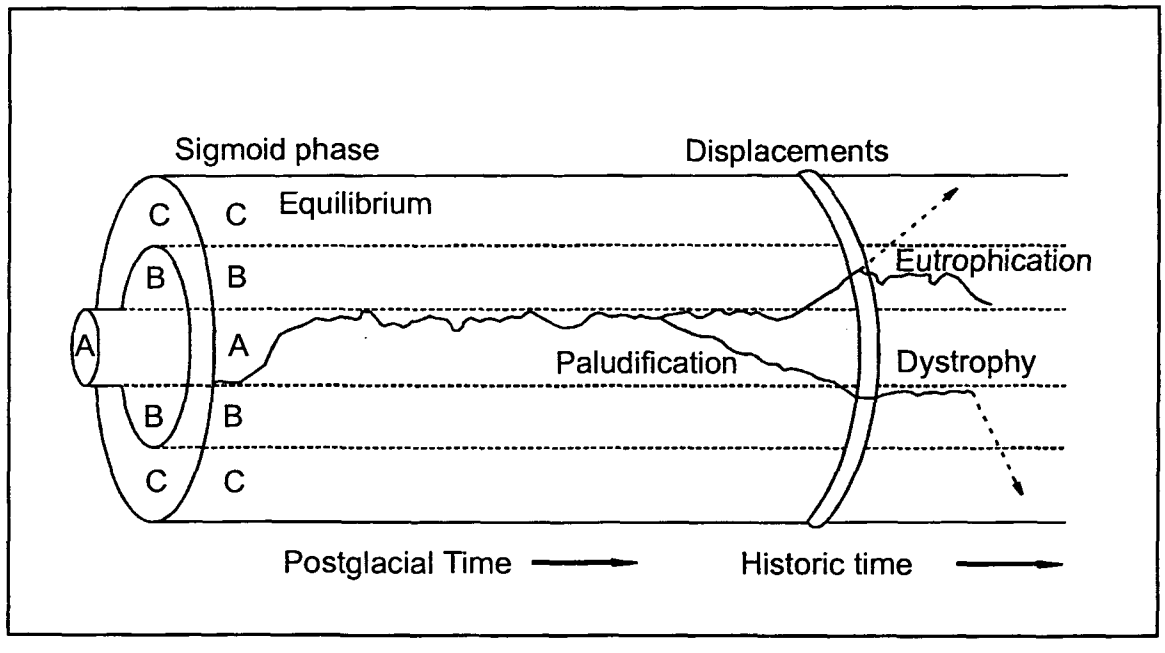


Figure 2.7 Stability of trophic equilibria in space-time, as inferred from ontogenies of eutrophic lakes, dystrophic and culturally eutrophied lakes. (Deevey, 1984)

Although reservoir formation is anthropogenically induced, the process of reservoir ecosystem development is analogous to the process of ontogeny described for natural lakes. When a river is blocked and a new body of water created, the recently flooded area will be extensive and the decomposition of uncleared litter and vegetation may create a temporary

anaerobic condition, which eliminates many aquatic organisms. The sediment and overlying water will have active exchanges of many biologically important elements, so that the water chemistry will be subject to rapid change. The shoreline will be unstable and wave action will cause extensive shoreline erosion, which may in turn lead to excessive temporary sedimentation. This is equivalent to the sigmoidal phase in Figure 2.7. The biological events at the initiation of a new reservoir may not persist. Aquatic insect production is often spectacularly high for a few years. In some reservoirs, the fish production increases rapidly, only to decline to lower sustainable levels as the reservoir reaches equilibrium (Taub, 1984; Hall *et al.*, 1999). Hall *et al.* (1999) reported that Lake Diefenbaker, Canada, exhibited typical lake ontogeny with three trophic periods as illustrated in Figure 2.7.

2.5.4 Managing phytoplankton in reservoirs

In productive water supply reservoirs there is a need to prevent or reduce the growth of planktonic algae (Brierley, 1984; Hayes & Greene, 1984). Algal production affects the operations necessary to treat water for supply. For example, the total biomass and composition of the phytoplankton affects the necessary treatment of raw reservoir water prior to its supply to consumers. Where there is minimal algal growth, treatment has comprised little more than disinfection (usually chlorination). However, where a greater concentration of algae is present, treatment becomes more costly because additional treatment processes (including filtration, coagulation and flotation) are required before the raw water is fit for public supply (Reynolds, 1999). The management of phytoplankton populations fall into three categories, invoking chemical, physical and biological approaches.

Physical approaches

Artificial destratification – aeration and the manipulation of reservoir mixing regimes

Artificial destratification, or artificial aeration, has been the most commonly applied physical technique used to control phytoplankton in reservoirs (Reynolds, 1999). This technique involves the destruction / prevention of the two-layer stratified structure which can develop naturally in a reservoir during the summer months. The most common method of artificial destratification is the introduction of compressed air through a perforated pipe or diffuser (Figure 2.8a). Commercial designs such as 'Helixor' tubes exist (Figure 2.8b), which are usually installed in the deepest areas of reservoirs and create a rising plume of bubbles that entrap bottom water and circulate it to the surface. A simpler alternative is the sinking of a pipe of flexible material with regular small perforations along its length along

the deepest axis of the reservoir connected to a source of compressed air. This creates a 'curtain' of bubbles. Both techniques destratify the immediate region of their operation and then progressively draw in water from further away until the full body is mixed (Harper, 1992).

The aim of artificial destratification is to maintain the reservoir in an isothermal condition, with temperature and dissolved oxygen content uniform throughout (Harper, 1992; Imboden, 1992). The quality of the water withdrawn for supply becomes independent of the depth from which it is taken (Henderson-Sellers, 1979). In addition, algal cells that would otherwise be confined to the narrow photic zone are circulated throughout the depth of the water column. This results in the algae experiencing a lower overall light regime and their photosynthesis and growth is inhibited, reducing productivity and peak algal numbers (Harper, 1992). This usually results in water of improved quality, which is thus easier to treat at the water treatment works (Whitton, 1979).

The biomass and species composition of the phytoplankton is extremely sensitive to the depth of mixing (Reynolds, 1999). Bloom-forming cyanobacteria, which are favoured by stable conditions, may be out-competed by species that thrive under conditions of vigorous or deep mixing (Steinberg, 1983). Van de Veer *et al.* (1995) reported the successful reduction in the abundance of bloom-forming *Microcystis* and *Aphanizomenon* populations in Nieuwe Meer, Amsterdam using artificial mixing. Steel (1972) and Toms (1987) reported similar results in reservoirs supplying water to London. These positive effects are of particular interest in water supply reservoirs, where the presence of toxins produced by cyanophytes, is of concern for public health.

Studies into the effects of aeration are limited and the literature consists mainly of research in natural lake environments. For example, Lindenschmidt & Chorus (1997) carried out research into the effects of aeration on stratification and phytoplankton populations in Lake Tegel, Berlin. Sandman *et al.* (1990) examined the effects of aeration on the eutrophication history of Lake Särkinen, Finland. Schladow & Fisher (1995) studied the physical response of temperate lakes to artificial destratification. Brierley (1984) investigated the effects of artificial aeration on algal populations in UK reservoirs. Reynolds *et al.* (1983, 1984) carried out a series of controlled experiments in limnetic enclosures using intermittent mixing to study algal species succession and concluded that, "the impact of artificial destratification on phytoplankton composition is reported to alter the "temporal phasing of compositional changes but not the fundamental sequences" (Reynolds, 1984b, p.115).

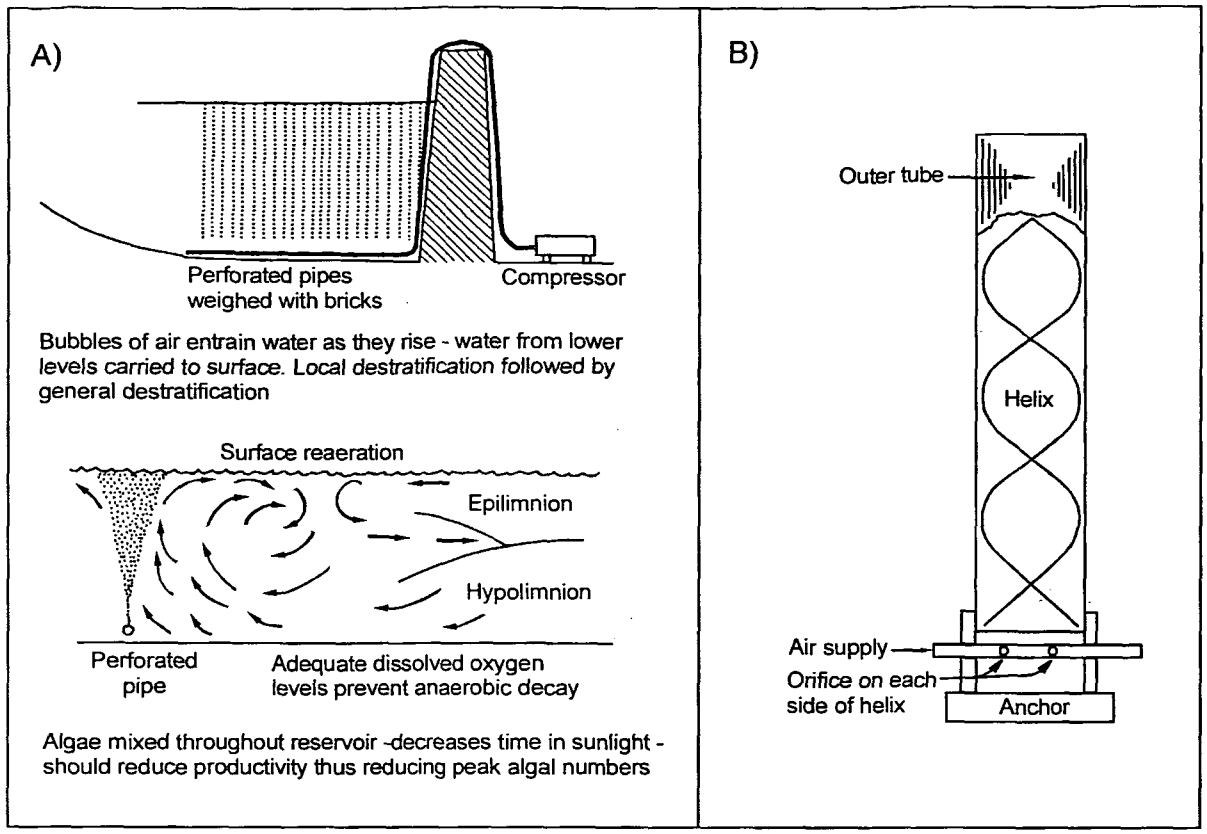


Figure 2.8 **Illustrations of artificial reservoir destratification methods; a) perforated pipe system for reservoir overturn and its principle of operation (modified from Brierley, 1984); b) A 'Helixor' tube for artificial overturn of reservoirs (modified from Tolland, 1977)**

Chemical approaches

Manipulating reservoir nutrient levels

Hayes *et al.* (1984) describe a number of different options for manipulating phosphorus levels in reservoirs. These include:

a) the use of shallow pre-reservoir basins in which prolific algal growth can reduce the nutrient loadings to the main reservoir

b) the construction of a physico-chemical phosphorus-removal works to treat the inflows to the reservoir

c) chemical treatment of input waters within a pre-reservoir

d) chemical treatment of the total reservoir body

e) chemical treatment of the waters entering the reservoir

f) diversion of nutrient-rich waters from the reservoir

The most widely used methods are described below:

Ferric sulphate (and copper sulphate) dosing of water entering the reservoir

In the UK, a large number of highly productive artificial lowland reservoirs have been treated by addition of copper or ferric sulphate. Chemical treatment using ferric sulphate facilitates precipitation of soluble phosphate from the water column to the sediments, thus reducing the availability of phosphorus for phytoplankton growth. This treatment method was documented for Foxcote reservoir, Buckinghamshire (Anglian Water) by Young *et al.* (1987). In 1981 a ferric sulphate dosing control programme was applied to the eutrophic pumped inlet water entering Foxcote from the River Great Ouse in order to alleviate water treatment problems through reduction of planktonic algal numbers. Initially, reservoir chlorophyll-*a* levels were considerably reduced. Subsequently however, regular prolific algal blooms occurred which were attributed to the re-solubilization of phosphorus from organic matter deposited on the surface sediments. Decay of this material caused a reduction in sediment oxygen content and led to further release of bound nutrient. This pattern of internal nutrient cycling eventually abated, but despite improvements in the quality of water supplied for treatment, the removal of plankton domination allowed rapid development of higher plants which themselves produced treatment problems (Daldorph, 1999).

Pre-treatment reservoirs

The nutrient-dependent carrying capacity of water can be reduced at the point of entry to the reservoir by chemical treatment, or alternatively inflow water can be pumped into pre-treatment reservoirs and chemically treated therein. This inhibits algal growth in the same way as dosing the total reservoir, however since chemicals do not enter the main body of the reservoir, they do not impact directly upon reservoir ecology. Ardleigh reservoir near Colchester has undergone phosphate stripping of its enriched riverine (River Colne) inflow for the last 20 years (Mike Suffling, AW, pers. comm.). The piped inflow is pumped into pre-treatment reservoirs and ferric sulphate is mixed with the water to reduce phosphate concentrations to consistently low levels, prior to release into the main reservoir.

Biological approaches

The use of barley straw to inhibit the growth of cyanophytes

Barley straw is put into the water column, where it starts to decompose. This decomposition releases lignins into the water, which are oxidised into humic acids. Under direct sunlight these humic acids combine with dissolved oxygen in the water to form hydrogen peroxide. Low levels of this chemical are known to inhibit the growth of algae. Thus, decomposition of the barley straw bales provides a low but continuous source of hydrogen peroxide for up to six months, although large numbers of bales (10 g of straw per m^2 of water surface area)

are required to achieve the desired effect (Barrett & Newman, 1992; Newman & Barrett, 1993). In recent years large numbers of barley straw bales have been placed in some reservoirs e.g. Cropston and Swithland (John Smith, STW, pers. comm.) and Porth reservoirs in the UK and have successfully alleviated problematic cyanophyte blooms.

Biomanipulation techniques

Biomanipulation relates to the anthropogenic alteration of organisms living at different trophic levels to bring about changes in ecosystem structure and function. This technique is based on the principle of cascading trophic interactions (Carpenter *et al.*, 1985) and usually relates to 'top-down' control of biomass and composition at the lower trophic levels (i.e. phytoplankton and zooplankton), by changing that at the higher trophic levels (i.e. fish). Most examples of the successful application of biomanipulation techniques to regulate phytoplankton abundance and manipulate trophic level interactions are reported from shallow lake ecosystems (e.g. Moss *et al.*, 1996). There are few examples of such techniques being applied deliberately to reservoirs (Reynolds, 1999). Benndorf (1992) reported on a series of controlled alterations to the food web of the Bautzen Reservoir, Germany and concluded that in reservoirs biomanipulation was only likely to be effective as an adjunct to nutrient reduction.

2.5.5 Impacts of reservoir draw-down on ecology

The edges of reservoirs often appear ugly, because there is little to see but mud or rock when water levels are low and large areas of bare sediment are exposed by draw down. The water level fluctuates according to demand and a closed cover of vegetation seldom develops in conditions where plants are sometimes submerged and sometimes exposed. The combination of floods in winter and spring and desiccation in summer and autumn presents an unstable environment that is unfavourable to the majority of species. However, this provides an important habitat for the few stress-tolerant plants that can take advantage of the combination of submergence and exposure. Perennial flowering plants that can tolerate these conditions include *Eleocharis palustris* L. (common spike-rush), *Hippuris vulgaris* L. (mare's-tail) and *Polygonum amphibium* L. (amphibious bistort). A tiny green alga, *Botrydium*, often covers the mud a couple of weeks after it is first exposed, especially in areas rich in lime and organic matter (Whitton, 1979). The uncommon *Juncus filiformis* L. (thread rush) grows in great abundance on the bare mud at Blackbrook reservoir when water levels are low (Mags Bainbridge, Leicestershire Wildlife Trust, pers. comm.). *Chara* spp. are pioneer species that are able to colonise suitable environments rapidly and in high

numbers (Blindow, 1992). All the aforementioned species benefit from the disturbance caused by fluctuating reservoir water levels.

2.5.6 Sedimentation patterns in reservoirs

Primary sedimentation processes

The formation and behaviour of lacustrine sediments is dominated by the interaction of a number of physical processes. Sediment deposits accumulating in lakes and reservoirs will comprise both autochthonous material that originated within the water body, such as the remains of aquatic organisms, and allochthonous material derived from external sources, such as sediment eroded from the surrounding drainage basin (Foster & Walling, 1994). In lowland reservoirs, the sedimentation of autochthonous material may be more rapid and thus of overall greater importance than the accumulation of allochthonous sediments seen in upland sites (Patrick & Stevenson, 1988).

In general, the volume of allochthonous material entering a reservoir is dependent upon the catchment sediment yield, which is related to factors such as catchment geology, topography, precipitation, land use and area. The quantity and range of autochthonous material will vary depending on the ecological characteristics of individual reservoirs, and is largely dependent upon water chemistry and the interactions between different levels of the trophic cascade, which can exhibit seasonal variation. The areal distribution of both autochthonous and allochthonous sediment is a function of particle size and texture, reservoir size and shape, reservoir inflow-outflow characteristics and reservoir operating characteristics (Shen, 1971; Davis, 1996).

The process by which allochthonous sediment settles in a reservoir is essentially the same as the sedimentation process that occurs in any body of fluid. As water enters the reservoir, the velocity decreases, turbulence is dampened out and entrained particles settle out and deposit as soon as the flow velocity drops below their terminal velocity (Annandale, 1987). Since many reservoir systems are formed from existing river systems, sedimentation normally begins at the entrance to the reservoir (Annandale, 1987). Typically the coarsest material (sands / gravels) is deposited first, forming a delta. This occurs in the shallow water areas, where the tributaries enter the lake (Sly, 1978). Finer material may also be deposited in the delta, but this fraction is normally carried further into the reservoir before it settles out and is usually found on the sections of the delta furthest from the point of inflow. Sediment may also remain suspended and pass through the reservoir in the form of a turbulent or colloidal suspension, or a density current (Davis, 1996).

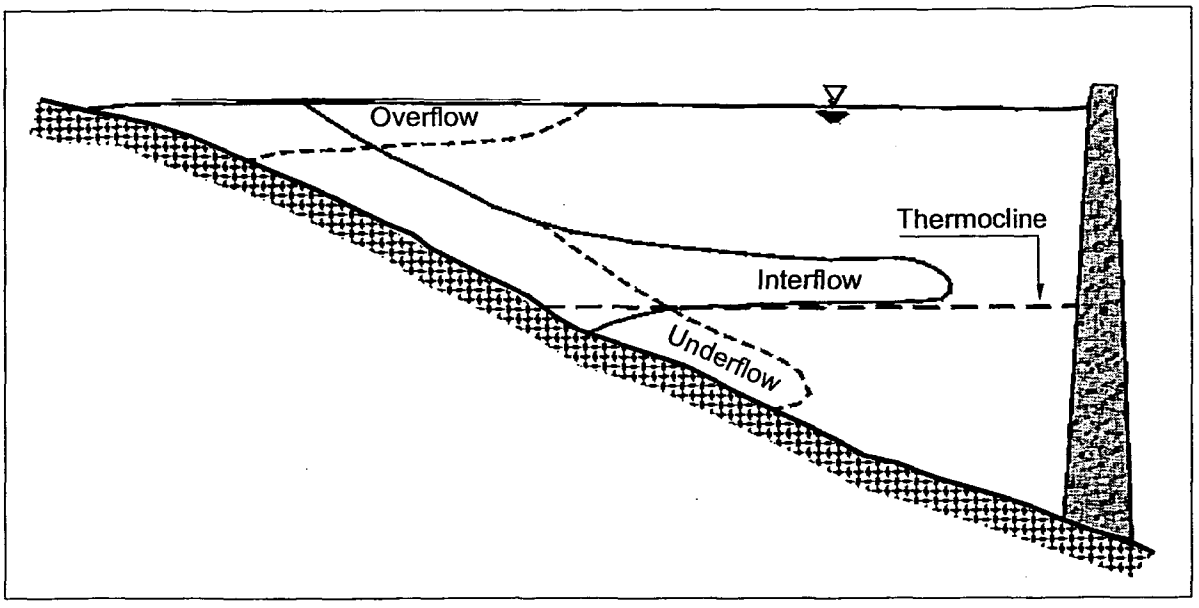


Figure 2.9 **Vertical focusing of flow in a stratified reservoir. The flow-through pattern may be characterized as overflow, interflow, or underflow depending on the density of the inflowing water relative to the vertical stratification structure in the impoundment (Morris & Fan, 1998)**

Primary sedimentation away from the delta front is governed by particle flocculation and settling. Figure 2.9 illustrates the vertical focussing of inflow in a reservoir. A major river inflow will generate a current for some distance into a lake. The inflowing water will tend to flow into that lake depth that matches its density, which is determined by a combination of the water's temperature and the effects of any dissolved and suspended materials entrained in it. Stratification can cause inflowing water to pass through a reservoir as overflow, interflow, or underflow, depending on the relative density of the inflow and the vertical density structure of the impounded water. Warm water will flow across cooler water as overflow, water of intermediate temperature will flow across the surface of the thermocline and cool, sediment-laden inflow will flow beneath warmer water as a bottom current. In some reservoirs, turbidity currents can transport a significant amount of sediment to the dam (Morris & Fan, 1998).

2.5.7 Secondary sedimentation processes and the use of reservoir sediments for palaeolimnological research

Secondary sedimentary processes in artificial reservoirs can be similar to those occurring in natural lakes, for example sediment focusing and bioturbation (Sly, 1978). However, reservoirs often exhibit complex and heterogeneous sediment accumulation patterns caused by frequent alterations of water level (drawdown) and the interaction of lacustrine and fluvial deposition (e.g. Fabre & Patau-Albertini, 1986). These processes can lead to

additional secondary sedimentation processes such as re-working of previously deposited material. Working on UK upland reservoirs in the Pennines, Patrick & Stevenson (1988) found that variability in the quality of the sediment record, compounded by high rates of sediment accumulation resulting from catchment erosion, severely affected the availability of suitably undisturbed stratigraphic sequences for palaeoenvironmental study. Thus in contrast to the well-preserved sediment records seen in most natural lakes (Battarbee, 1999), sedimentary sequences from reservoirs often show hiatuses and subsequent loss of stratigraphic conformity, although these can usually be accounted for if they are acknowledged as potential problems from the outset (e.g. Tibby, 2000).

The three characteristic sedimentary zones documented by Stott (1984) for upland reservoirs (Figure 2.10), suggest that coring locations for palaeolimnological work should be restricted to the more marginal areas of the intermediate zone, away from the scour channel. However, this supposition was made in relation to upland and not lowland reservoirs. Although the same theory may apply to lowland reservoirs, there is no available research to support this presumption. In the UK, with the exception of the upland reservoir studies of Stott (1984) and Patrick & Stevenson (1988), there has been only limited use of reservoir sediments for palaeoenvironmental reconstructions and as such there have been few attempts to assess the potential of reservoirs for such purposes.

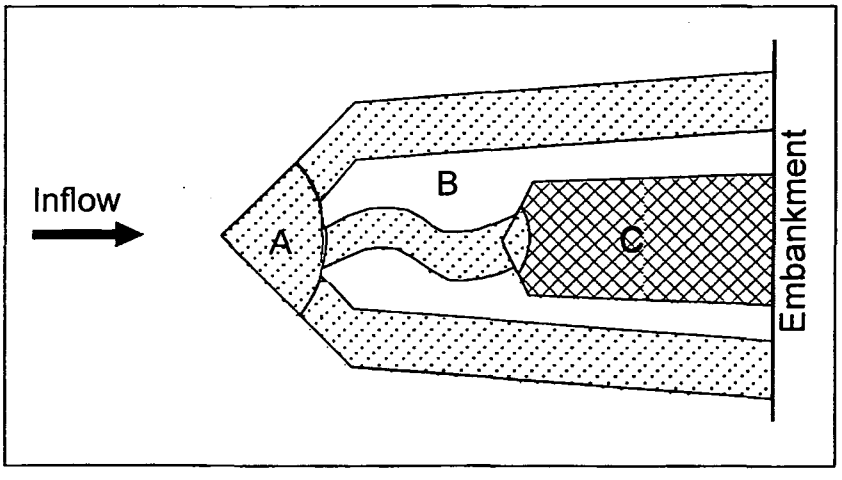


Figure 2.10 **The three characteristic sedimentary zones described for upland reservoirs (Stott, 1984). A = Shallow water zone, characterised by high, but spatially discontinuous rates of sedimentation and extensive re-working during drawdown; B = Intermediate zone of moderate exposure during drawdown. Re-working is confined to the scour channel that has temporary storage of coarse sediment. Marginal sediments in this zone predominantly result from primary sedimentation with little erosion and re-working, although sedimentation may not be continuous. C = Deep water zone rarely exposed by draw-down, with low rates of primary sedimentation, but receiving extensive re-worked sediments from upstream, with occasional but major erosional hiatuses.**

It is common practice to assess the quality of the sediment record at study sites before embarking on detailed sediment core analysis (Battarbee, 1999). Usually the central deepest part of a lake is assumed to provide a representative location for the analysis of diatom assemblage changes over time since this is usually the area of sediment focussing (Battarbee, 1986). Thus for the assessment of compositional trends, analysis of a single core is usually sufficient, although it is useful to obtain a range of cores from different locations in the lake basin, so that the best core can be chosen for detailed analysis (Battarbee, 1999). This would normally be the core with the least disturbance and the most rapid sediment accumulation rate (Allott *et al.*, 1992). Lake morphometry and depositional processes can create within-lake variability and thus multi-core studies are usually necessary for the accurate determination of diatom abundance and accumulation rates (Anderson *et al.*, 1993; Anderson, 1998).

There have been few detailed studies of diatoms in reservoirs in terms of their sedimentary records - the work of Patrick & Stevenson (1988) on UK upland reservoirs, that of Dixit *et al.* (1999) on North American reservoirs and that of Tibby (2000, 2004) on lowland southeast Australian water storages are isolated examples. Substantially more references exist for modern ecological diatom work in reservoirs. For example, Leitão & Léglize (2002) studied epilimnetic phytoplankton composition during the inaugural 10 years of operation in the artificial Vieux-Pré reservoir, northeast France; Gómez *et al.* (1995) studied Spanish reservoir phytoplankton assemblages; Atkinson (1988) observed phytoplankton assemblages in the newly created Cow Green (Upper Teesdale) reservoir and Wilson *et al.* (1975) examined reservoir phytoplankton composition in Chew Valley and Blagdon Lake (Bristol). However there is a distinct paucity compared with the volume of limnological research published for natural lakes. Consequently, the tools that have been applied to infer environmental change in natural lakes, such as the creation of diatom-based calibration sets and the development of inference models, have thus far only received limited attention in reservoirs. One exception is the diatom-inferred TP (DI-TP) inference model created by Tibby (2004) for lowland southeast Australian water storages, which was successfully tested on a sediment core from Burrinjuck Reservoir using long-term monitoring data (Tibby, 2000). Reynolds (1984b, 1999) observed that the phytoplankton species assemblages seen in both natural lakes and artificial waterbodies are in many ways similar. Both the palaeolimnological research of Tibby (2000; 2004) and the limnological observations of Reynolds (1984b, 1999) suggest that further palaeolimnological work in artificially created reservoir environments is feasible and application of such research to the reconstruction of nutrient histories should be of relevance in both artificial and natural waterbodies.

PART TWO

Research Approach & Methodology

CHAPTER THREE

Methodology

3.1 Introduction

This chapter outlines the reservoir site selection procedure and details the sampling methodologies and data analysis techniques employed in this study. The chapter is divided into three sections. The first introduces the calibration dataset and long-coring sites and the process of their selection. The second discusses both the field and laboratory methodologies employed in the collection, processing and analysis of water, sediment and phytoplankton samples. The final section examines the techniques employed to interpret and display the resultant data, including details of the statistical methods and graphing tools utilised.

3.2 Site selection procedure

3.2.1 Calibration dataset

General considerations

To build a calibration dataset of UK lowland reservoirs a suite of suitable sites was first required. Davis and Smol (1986) suggest that to create any such calibration dataset a minimum of 30 sites are required. Small datasets are suggested to limit the performance of diatom-based inference models (Hall *et al.*, 1999), although Tibby (2004) showed that there was no simple relationship between model performance and dataset size.

In selecting sites, four main factors were considered important; reservoir location and accessibility, reservoir physical and chemical characteristics, availability of undisturbed surface sediments for sampling and the availability of background information regarding recent history and site management practices.

To meet the overall objectives of the current study all sites were required to be surface water artificial lowland reservoirs located within the United Kingdom (UK). 'Surface water' relates to water storage facilities located above-ground. Reservoirs were deemed 'lowland' if they were located, with reference to Ordnance Survey (O.S.) maps, at an altitude of ≤250 metres above Ordnance Datum (m.a.O.D.). 'Artificial' relates to the man-made origin of the reservoirs. In the UK, this corresponds to the following reservoir types, a) waterbodies which have been created artificially by the construction of a dam across a flowing river or stream (impounding reservoirs); b) waterbodies fitting the aforementioned description but

whose water sources are augmented by water pumped in from outside the natural catchment (pump-storage reservoirs); c) waterbodies which are a combination of impounding and pump-storage (mixed); and d) impoundments created to capture spring-water sources (spring). All reservoirs within the current study fit one of the above descriptions.

For inclusion in the calibration set all reservoirs should ideally perhaps have been of the impounding type, because this type of reservoir is fed only by water flowing directly from the surrounding catchment, therefore the water source is known and in-reservoir limnological conditions can be more easily explained and interpreted. However, only 22 of the reservoirs available in the current study met this criterion. This was considered an insufficient number of sites for the formation of a calibration dataset and from which to subsequently develop inference models. Therefore reservoirs pertaining to all the aforementioned types were considered for inclusion in the calibration dataset.

Location and accessibility

The 46 selected reservoir sites (Figure 3.1) were dispersed over a large area of lowland England and encompassed almost the entire suite of UK lowland reservoirs. The sites appear to be clustered into groups. This was not based upon a conscious decision, but instead reflects regional geology and hence suitability for the construction of surface water storage facilities. However, the clustering of sites was a useful feature to exploit logistically; enabling greater fieldwork efficiency, with more time available for sampling and less time expended travelling between sites.

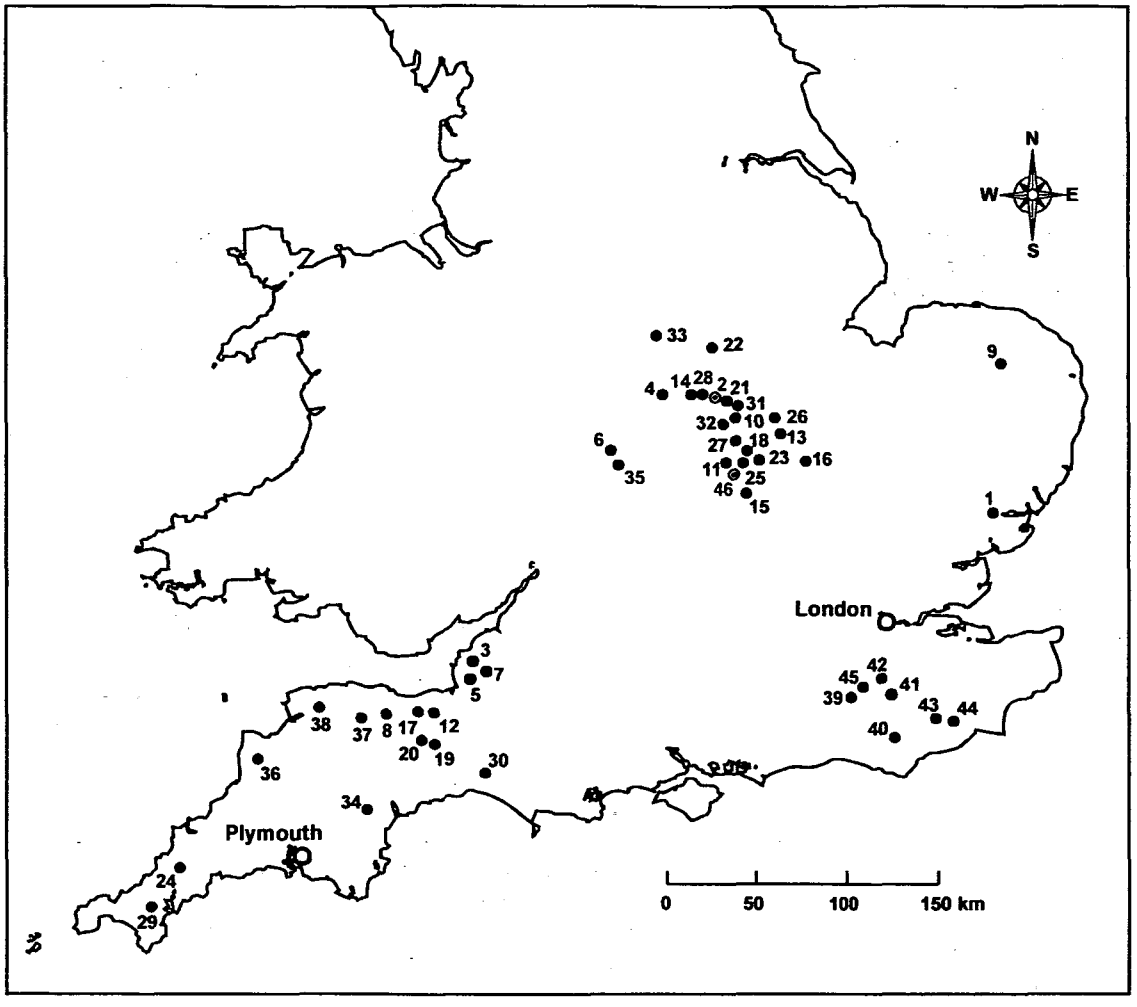
The 46 reservoirs were owned and/or managed by ten different Water Companies. For each site the relevant personnel were approached to gain access permission and to discuss Health and Safety issues. Sites were required to be accessible for boat-based fieldwork. At many sites arrangements were made with Water Company personnel or on-site fisheries and sailing / waterskiing club staff which enabled use of on-site motor or rowing boat facilities. However, for sites where no facilities were available both inflatable and rigid rowing boats were transported from site-to-site to enable deployment of the craft most appropriate to the site and prevailing weather conditions. Care was taken to clean all equipment thoroughly to avoid cross-contamination and dispersal of organisms between reservoirs.

Physical and chemical characteristics

To meet the original aims of the study, sites were selected to span a broad trophic gradient. This was designed to increase the ultimate performance of the diatom-based models

developed for the inference of trophic variables. Chemical and physical criteria were established to shorten gradients in the calibration set of environmental variables with a well-documented influence on diatom taxon responses. The environmental criteria were set as follows:

- pH ≥ 6.5
- EC $\leq 1000\ \mu Scm^{-1}$
- Depth (max.) ≥ 5.0 m
- Age ≥ 20 years



1.	Ardleigh	13.	Eyebrook	25.	Ravensthorpe	37.	Wimbleball
2.	**BLACKBROOK**	14.	Foremark	26.	Rutland	38.	Wistlandpound
3.	Blagdon	15.	Foxcote	27.	Stanford	39.	Ardingly
4.	Blithfield	16.	Grafham	28.	Staunton Harold	40.	Arlington
5.	Cheddar	17.	Hawkridge	29.	Stithians	41.	Bewl
6.	Chelmarsh	18.	Hollowell	30.	Sutton Binghan	42.	Bough Beech
7.	Chew Valley	19.	Leigh	31.	Swithland	43.	Darwell
8.	Clatworthy	20.	Luxhay	32.	Thornton	44.	Powdermill
9.	Costessey	21.	Nanpantan	33.	Tittesworth	45.	Weir Wood
10.	Cropston	22.	Ogston	34.	Trenchford	46.	**DAVENTRY**
11.	Draycote	23.	Pitsford	35.	Trimpley		
12.	Durleigh	24.	Porth	36.	Upper Tamar		

Figure 3.1 Locations of the UK lowland reservoir calibration set and long-coring sites (sites in BOLD are long-coring sites).

The ultimate aim of the current study was to develop models to infer open-water chemical conditions. Anderson *et al.* (1993); Bennion (1994); Siver (1999) and Bradshaw *et al.* (2002) noted that inclusion of non-planktonic taxa might add error to inference models by confounding diatom-total phosphorus relationships. Tibby (2004) suggested that the relatively strong performance of a DI-TP model for southeastern Australian water storages might in part have been attributed to the dominance of plankton in most sites. The depth of the reservoirs in the current study was therefore set at ≥5.0m to try to ensure that the maximum depth exceeded the euphotic depth resulting in reservoir diatom communities with limited development of non-planktonic taxa but domination by planktonic taxa - considered most responsive to epilimnetic conditions.

To minimise the influence of the well documented effects of pH (e.g. Birks *et al.*, 1990) on the distribution of diatom taxa, the pH minimum was set at ≥6.5. This is a similar minimum to those specified in comparable studies. For example, Kauppila *et al.* (2002) focussed on sampling as long a trophic gradient as possible, sampling 68 lakes spanning a pH gradient of 6.6-9.2 (mean =7.1). Similarly, Tibby (2004) sampled a long trophic gradient which spanned a pH range of 6.8–8.9. Other authors have narrowed the pH range further e.g. Hall & Smol (1992) narrowed the pH range to values between 7.5 and 8.5, although the trophic gradient was correspondingly short.

Only 'freshwater' sites were selected for inclusion in the calibration set. Sites were deemed 'freshwater' if their electrical conductivity (EC) was ≤1000 μScm^{-1}. All potential reservoir sites fulfilled this criterion.

The age of the reservoirs was set at ≥20 years to increase the likelihood of the water bodies having passed through the period of instability usually experienced subsequent to initial filling, a process analogous to the earliest stage of ontogeny in natural lakes.

Sediment disturbance

To assist in the selection of suitable sediment coring sites, information was gleaned from as many sources as possible. Prior to sediment sampling, reservoir managers were approached for depth contour maps of each reservoir, along with information concerning draw-down, destratification, scouring and other management activities which could potentially lead to disturbance of reservoir sediments.

In relation to draw-down, it was valuable to have seen each reservoir over all seasons. A number of sites experienced significant draw-down and bank-side exposure during the late summer / early autumn. Knowledge of the potential extent of sediment exposure was important to ensure that the sampling of surface sediments avoided any areas which had been recently exposed. This reduced the possibility of extracting surface sediment samples from areas where drawdown had disturbed the sediments and instigated drying, cracking and reworking. In many cases contour maps were available (in particular for AW, STW and WW) and were valuable for locating suitable coring sites, enabling a compromise between the deepest, but also potentially least disturbed areas of sediment focussing.

Background information

Background information concerning recent reservoir history and management practices was important to aid interpretation of any idiosyncrasies in the environmental or species data collected for each site and to ensure the integrity of the study's results. Considerable anecdotal information could be obtained from on-site personnel in addition to the tabulated data provided by Water Company site managers and off-site personnel.

Table 3.1 details the locations and morphometric, catchment and other characteristics of the 46 calibration set reservoirs. Grid references, altitudes, surface areas, catchment areas and catchment land-use details were obtained with reference to the appropriate O.S. maps or (for a few sites) from information provided by Water Companies. Underlying catchment geology was determined with reference to Geological Survey maps. Information relating to reservoir ages, types, depths, capacities and the presence or absence of destratification equipment was provided by Water Companies. The tabulated characteristics are discussed in full detail in Chapter 4.

3.2.2 Long-coring sites for inference model application

Blackbrook and Daventry reservoirs (Figure 3.1) are included in the 46-reservoir calibration dataset but were also selected as suitable sites for long-coring and subsequent application of the inference models created in this study. Their selection was based on several factors including the relatively long length of their sediment record and evidence of good fossil diatom preservation. Detailed reasoning behind the selection of these sites for long-coring is discussed in Chapter 8 (section 8.2). Long cores were also taken from Chew Valley and Blagdon reservoirs, but were not considered suitable for inference model application (see section 8.2 for reasoning).

No.	Reservoir name	Water co.	Grid reference	Date completed	Age (Yrs)	Res type code	Geology code	De-strat?	Altitude (m.a.O.D)	Catchment area (km^2)	Catchment land-use %Agri	%Urban	%Decid	%Conif	%Res	Surface area (km^2)	Capacity (Ml)	Depth max.(m)	Depth mean(m)	Res Time Days
1	Ardleigh	AW	TM 034282	1979	21	2	3	Yes	33	12.40	75.5	5.0	12.5	2.5	4.5	0.554	2200	14.0	3.9	200
2	Blackbrook	STW	SK 458175	1906	94	1	2	Yes	111	12.20	81.3	0.0	9.0	7.0	2.7	0.325	2300	18.3	7.1	
3	Blagdon	BWW	ST 515598	1901	99	1	3	Yes	45	24.80	84.8	1.0	5.5	1.5	7.2	1.780	8450	11.5	4.3	240
4	Blithfield	SSW	SK 073229	1953	47	1	3	Yes	95	109.30	87.1	6.0	2.5	1.5	2.9	3.197	18170	14.5	5.6	363
5	Cheddar	BWW	ST 441538	1938	62	0	3	Yes	18	0.94	0.0	0.0	0.0	0.0	100.0	0.937	6050	14.0	6.5	
6	Chelmarsh	SSW	SO 738875	1966	34	3	2	No	69	1.00	56.0	0.0	5.0	0.0	39.0	0.390	3060	25.6	7.8	
7	Chew Valley	BWW	ST 570600	1953	47	1	3	Yes	56	51.30	80.5	2.0	4.0	4.0	9.5	4.860	20500	11.5	4.3	255
8	Clatworthy	WW	ST 044312	1959	41	1	1	Yes	226	18.20	86.1	1.0	5.0	5.0	2.9	0.526	5364	27.6	10.2	
9	Costessey	AW	TG 163129	1940	60	3	3	No	3	0.05	0.0	0.0	0.0	0.0	100.0	0.049	147	5.0	3.0	
10	Cropston	STW	SK 546109	1870	130	2	2	No	81	18.00	68.1	2.0	12.0	15.0	2.9	0.530	2528	11.9	4.8	
11	Draycote	STW	SP 460700	1969	31	3	3	Yes	94	5.61	45.7	10.0	0.5	0.5	43.3	2.430	22730	17.4	9.4	
12	Durleigh	WW	ST 274363	1939	61	2	3	Yes	22	17.30	85.2	0.0	3.5	9.5	1.8	0.314	959	8.2	3.0	
13	Eyebrook	CDW	SP 854955	1940	60	1	3	No	68	60.10	88.3	1.0	6.5	1.5	2.7	1.640	8096	12.7	5.3	
14	Foremark	STW	SK 328240	1977	23	3	3	Yes	107	2.95	68.5	0.0	0.0	0.0	31.5	0.930	13190	27.7	14.2	
15	Foxcote	AW	SP 713362	1956	44	1	3	No	110	2.81	78.2	0.0	15.0	0.0	6.8	0.190	500	5.0	2.6	
16	Grafham	AW	TL 150680	1966	34	3	3	Yes	43	15.58	52.1	2.0	5.0	0.0	40.9	6.380	58000	20.1	8.7	260
17	Hawkridge	WW	ST 212364	1964	36	1	2	Yes	100	10.90	77.8	0.0	11.0	10.0	1.2	0.129	864	19.8	6.7	
18	Hollowell	AW	SP 688728	1938	62	1	3	Yes	114	9.80	89.2	0.0	2.5	2.5	5.8	0.567	2100	10.0	3.5	550
19	Leigh	WW	ST 197178	1893	107	0	3	No	159	0.30	42.7	0.0	10.0	40.0	7.3	0.022	120	11.6	5.5	
20	Luxhay	WW	ST 203178	1905	95	2	3	Yes	145	1.00	22.7	0.0	47.5	22.5	7.3	0.073	547	17.8	7.5	
21	Nanpantan	STW	SK 507171	1870	130	1	2	No	86	4.30	74.3	0.0	14.0	11.0	0.7	0.032	132	6.7	4.1	
22	Ogston	STW	SK 377602	1960	40	2	2	No	119	26.67	91.1	1.0	5.0	0.0	2.9	0.770	6180	18.1	8.0	
23	Pitsford	AW	SP 775695	1956	44	2	3	Yes	90	52.00	90.2	3.0	0.5	0.5	5.8	3.035	17700	14.5	5.2	430
24	Porth	SWW	SW 805601	1960	40	1	2	No	28	22.25	90.3	4.0	5.0	0.0	0.7	0.153	514	8.0	3.4	
25	Ravensthorpe	AW	SP 678707	1890	110	1	3	Yes	106	11.90	91.1	0.0	5.0	0.0	3.9	0.460	1900	8.0	3.6	410
26	Rutland	AW	SK 932075	1977	23	3	3	Yes	84	74.00	67.0	7.0	5.5	3.5	17.0	12.600	124000	31.6	9.3	630
27	Stanford	STW	SP 602805	1928	72	1	3	No	110	56.00	95.0	2.0	1.5	0.5	1.0	0.550	1527	8.7	2.8	

Table 3.1 Characteristics of the UK lowland reservoir calibration set sites

No.	Reservoir name	Water co.	Grid reference	Date completed	Age (Yrs)	Res type Code	Geology Code	De-strat?	Altitude (m.a.O.D)	Catchment area (km^2)	Catchment land-use %Agri	%Urban	%Decid	%Conif	%Res	Surface area (km^2)	Capacity (Ml)	Depth max.(m)	Depth mean(m)	Res Time Days
28	Staunton Harold	STW	SK 380242	1966	34	3	3	Yes	75	26.00	82.7	0.0	13.5	0.5	3.3	0.850	6655	22.3	7.8	
29	Stithians	SWW	SW 715364	1967	33	1	1	Yes	160	9.50	86.3	2.0	0.0	0.0	11.7	1.110	5205	16.0	4.7	
30	Sutton Bingham	WW	ST 556115	1956	44	1	3	Yes	56	30.30	92.2	1.0	5.0	0.0	1.8	0.560	2614	13.4	4.7	
31	Swithland	STW	SK 559142	1894	106	2	2	No	58	14.80	64.5	2.0	18.5	9.5	5.5	0.810	2228	9.2	2.8	
32	Thornton	STW	SK 473075	1854	146	1	3	No	122	12.00	74.5	8.0	13.0	2.0	2.5	0.300	1320	10.6	4.4	
33	Tittesworth	STW	SJ 992595	1963	37	1	2	Yes	200	28.20	90.3	0.0	4.0	3.0	2.7	0.760	6440	20.6	8.5	
34	Trenchford	SWW	SX 805824	1907	93	1	1	No	240	4.00	37.0	0.0	0.0	60.0	3.0	0.120	909	14.0	7.6	
35	Trimpley	STW	SO 770788	1971	29	3	2	No	30	0.10	0.0	0.0	0.0	0.0	100.0	0.100	936	12.8	9.4	
36	Upper Tamar	SWW	SS 286120	1976	24	1	2	No	150	13.75	92.6	0.0	5.0	0.0	2.4	0.330	1335	10.0	4.1	
37	Wimbleball	SWW	SS 970307	1979	21	1	1	Yes	235	29.00	86.8	0.0	3.0	5.0	5.2	1.510	21320	35.0	14.1	
38	Wistlandpound	SWW	SS 645418	1953	47	2	1	No	240	3.40	85.0	0.0	0.0	10.0	5.0	0.170	1550	20.0	9.1	
39	Ardingly	SEW	TQ 332291	1979	21	2	2	No	50	21.50	46.4	0.0	25.0	25.0	3.6	0.780	4773	14.0	6.1	
40	Arlington	SEW	TQ 534073	1971	29	3	2	Yes	0	0.64	2.4	0.0	21.0	0.0	76.6	0.490	3500	11.3	7.1	
41	Bewl	SW	TQ 678332	1975	25	3	2	Yes	70	22.10	64.4	0.0	10.0	10.0	15.6	3.437	31370	29.4	9.1	
42	Bough Beech	SESW	TQ 493479	1968	32	3	3	Yes	60	6.90	71.9	0.0	5.0	5.0	18.1	1.250	13750	17.5	11.0	
43	Darwell	SW	TQ 717213	1950	50	2	2	Yes	40	9.30	39.4	0.0	26.5	26.5	7.6	0.708	4600	14.0	6.5	
44	Powdermill	SW	TQ 800195	1932	68	2	2	Yes	20	4.80	29.6	0.0	33.0	33.0	4.4	0.210	855	10.6	4.1	
45	Weir Wood	SW	TQ 402351	1953	47	1	2	Yes	70	3.40	37.8	3.0	13.0	13.0	33.2	1.130	5623	11.0	5.0	
46	Daventry	BWB	SP580639	1804	196	1	3	No	120	8.06	14.0	81.3	0.5	0.5	3.7	0.297	891	8.0	3.0	

AW: Anglian Water; **BWW**: Bristol Water Works; **CDW**: Corby & District Water Company; **SEW**: South East Water; **STW**: Severn Trent Water; **SW**: Southern Water; **SWW**: South West Water; **WW**: Wessex Water; **SESW**: Sutton & East Surrey Water; **BWB**: British Waterways Board

Reservoir type code: **0** = spring; **1** = impounding; **2** = combination of impounding and pumped storage; **3** = pumped storage

Geology: **1** = acidic; **2** = neutral; **3** = alkaline

Table 3.1 Characteristics of the UK lowland reservoir calibration set sites

3.3 Field and laboratory methodologies

3.3.1 Environmental variables

Sampling frequency

Many calibration sets are based on only one or two water chemistry data points (cf. Davis and Smol, 1986), yet many authors discuss the importance of representative water chemistry data for the generation of the most accurate predictive equations (Birks, 1998). Hanna & Peters (1991) highlight the importance of a sampling protocol which minimises variance associated with the mean and the bias associated with spatial and temporal variation. They conclude that representative sampling for a given lake requires several visits within a season. However few studies (e.g. Tibby, 2004; Bradshaw & Anderson, 2001) have access to intensive water quality data monitored at better than monthly resolution. In some studies environmental data are based on only one measurement (e.g. Hall & Smol, 1992; Fritz *et al.*, 1993b; Kauppila *et al.*, 2002). However, in the majority of studies the temporal resolution of the environmental data lie somewhere between these two extremes. The sampling protocol employed in the current study follows the recommendation of Bennion & Smith (2000) that a minimum of four seasonal samples should be taken for the calculation of representative average annual values. However it was not logistically possible to meet the monthly sampling regime advised by Battarbee *et al.* (2001) for nutrient calibration sets.

Variable	May '99	Jul '99	Oct '99	Jan '00	Mar '00	Jun '00	Oct '00
§ SD	•	•	•	•	•	•	•
Temp	•	•	•	•	•	•	•
pH	•	•	•	•	•	•	•
Alk	•	•	•	•	•	•	•
EC	•	•	•	•	•	•	•
Na^+				•			
K^+				•			
Cl^-				•			
Ca^{2+}				•			
Mg^{2+}				•			
SRP	•	•	•	•	•	•	•
TP	•	•	•	•	•	•	•
TON	•	•	•	•	•	•	•
TN	•	•	•	•	•	•	•
Chla	•	•	•	•	•	•	•
Si	•	•	•	•	•	•	•

Table 3.2 **Physical and chemical variables measured in the calibration set reservoirs (• variable measured at this time). § SD could not be measured in all reservoirs in all seasons.**

The 46 calibration set sites were visited on seven occasions every two to three months between May 1999 and October 2000. The sampling frequency in this study represents a

compromise between the logistical constraints imposed by a large number of sites across a wide geographical area, and the acquisition of a representative estimate for the mean annual water chemistry at each site.

The concentrations of plant nutrients such as nitrogen and phosphorus are highly dynamic because they may be utilized, stored, transformed, and excreted rapidly and repeatedly by the various aquatic organisms. In contrast, nutrients such as magnesium and sodium experience less seasonal variation (Wetzel & Likens, 2000). The sampling protocol illustrated in Table 3.2 reflects the differing seasonal dynamics of the various chemical and physical variables.

Environmental data quality and consistency

"A reliable comparison of the lakes with each other is possible only if the measurements of lake properties take place under comparable circumstances" (Huttunen & Meriläinen, 1983). This argument delivers support to the current study's chosen sampling protocol. Despite a small number of Water Companies collecting regular, comprehensive chemical data using comparable methods, the majority utilise their own preferred methodologies, resulting in differing sampling strategies, detection limits and temporal data resolution. This makes comparison of results from different regional Water Companies more difficult, and could lead to bias in the dataset. Despite this study's relatively coarse sampling frequency, the standard methods employed help to maintain internal consistency, thus enabling reliable between-site comparisons. A further point worth noting is that at the time of sampling the majority of Water Companies did not carry out total phosphorus (TP) analyses. Since measurement of this variable is pertinent for eutrophication studies and shows potential for the development of inference models, collection of an independent suite of water chemistry data was further justified.

Most water companies maintain records of the major chemical determinants (e.g. pH) on a more regular basis than would ever be logistically possible in a study of this geographical scale. With the generous provision of data from the various Water Companies involved in this study, it is possible, for selected variables, to compare the representativeness of their more extensive dataset with that derived from the lower frequency sampling strategy employed in this study.

Water sample collection and treatment – general methodology

Water samples for both field and laboratory analyses were taken from the epilimnion at approximately 0.5 m below the water surface in as deep and undisturbed location as possible. Hilton *et al.* (1989) compared the results of nutrient analyses on samples taken using different methods. They concluded that as long as point sources of pollution and areas of sediment resuspension are avoided, edge samples were quite adequate. In the current study, sampling from a boat was possible on most occasions. However when this was prevented due to poor weather conditions, samples were taken from as deep and undisturbed water as could be sampled from the shore by throwing a weighted sampling bottle out into the reservoir on a 10 m length of rope.

Subsequent analyses for different environmental variables required collection of both filtered and unfiltered water samples. All samples were stored in 125 ml HDPE acid-washed (10% HCL) bottles prior to laboratory analysis. Unfiltered samples were collected by first rinsing the bottle thoroughly with reservoir water, then dipping the bottle below the water surface, allowing it to fill, and finally fitting the lid whilst underwater to avoid air entrapment and sample deterioration; no preservative was added. Filtered samples were collected by passing a known volume of water (usually 150 ml) through a Whatman™ WCN (cellulose nitrate) 47 mm diameter, 0.45 μm pore size membrane filter under vacuum using a Nalgene™ 250 ml capacity filtration unit and hand pump. Samples were filtered in the field as soon as possible after collection to avoid conversion of dissolved substances into particulate form. Care was taken to avoid cross-contamination by thoroughly rinsing all filtration apparatus with distilled, deionised water (DDW) between samples. In addition to collection of the samples described above, 30 ml Bibby Sterilin® tubes were filled with unfiltered and filtered water from each reservoir on each occasion and deep-frozen as both a back-up and in the event of further analyses requirements at a later date. These samples are stored at the University of Plymouth.

Although storage of water samples before analysis should be avoided or at least minimised (Wetzel & Likens, 2000), the logistics of the current study's sampling programme prevented immediate determination of water chemistry. Whenever there was a delay prior to analyses, samples were stored in the dark at 4-5°C in a portable refrigerator.

Analytical methodologies for specific water chemistry variables

Table 3.3 lists the water chemistry variables measured in the current study. The table details where the samples were measured (field or laboratory), whether measurements were carried

out on filtered or unfiltered water samples, the range and detection limits of the analytical methods employed, and any dilutions required prior to analysis. All water chemistry analyses were carried out by the author in the Department of Geographical Sciences at the University of Plymouth (except Ca^{2+} and Mg^{2+} determinations which were carried out by Alex Bowden in the Department of Environmental Sciences at the same institution).

Variable	Filt. / Unfilt.	Field / Lab	Units	Range of method	Detection limit	Dilutions
pH	Unfilt.	Field	pH	1 – 11 (general purpose probe)	0.01	none
EC	Unfilt.	Field	μScm^{-1}	0 - 1000	+/- 10	none
Alk	Unfilt.	Lab	mgl^{-1} as $CaCO_3$	20 – 200 (using 0.02N HCl for titration)	1.73 (sensitivity 10)	none
Na^+	Filt.	Lab	mgl^{-1}	0 - 10	0.1	up to 1:4 (most 1:2)
K^+	Filt.	Lab	mgl^{-1}	0 - 10	0.1	none
Cl^-	Filt.	Lab	mgl^{-1}	*AAII: 0 - 20	0.1	up to 1:5 (most 1:3)
Ca^{2+}	Filt.	Lab	mgl^{-1}	0 - 1	0.001	mostly 1:100
Mg^{2+}	Filt.	Lab	mgl^{-1}	0 - 1	0.001	mostly 1:100
SiO_2	Filt.	Lab	mgl^{-1}	a) *AAII: 0 – 10 (May'99 - Jun'00)	0.002	up to 1:2 (most none)
				b) *AAIII: 0 - 20 (Oct'00)	0.01	none
TON	Filt.	Lab	mgl^{-1}	a) *AAII: 0 – 0.5 (May'99 - Jun'00)	0.008	1:20
				b) *AAIII: 0 - 10 (Oct'00)	0.02	none
TN	Unfilt.	Lab	mgl^{-1}	a) *AAII: 0 – 0.5 (May'99 - Jul '99)	0.008	1:20
				b) *AAII: 0 – 10 (Oct'99 - Oct'00)	0.02	none
SRP	Filt.	Lab	μgl^{-1}	*AAII & AAIII: 0 – 1000	5	none
TP	Unfilt.	Lab	μgl^{-1}	*AAII & AAIII: 0 – 1000	5	none

Table 3.3 Range and detection limits of the water chemistry methods (* AAII & AAIII are 'AutoAnalyser' automated chemical analysis machines)

Field measurements

pH

pH is a measure of the acidity or alkalinity of a sample on a scale from 0 (acid), through 7 (neutral) to 14 (alkaline). The farther the pH value from neutral (7), the greater the concentration of either H^+ or OH^- ions. pH is measured as a logarithmic value, therefore each integer represents an H^+ concentration ten times that of the next, higher number. Consequently average pH values are calculated from the antilogarithms (concentration units) (Wetzel & Likens, 2000). pH was measured using a Russell™ general purpose, combination, liquid-filled probe (CT711/LCW) with pH range 1-11. Measurements were made in the field by bringing unfiltered samples to 20°C before measurement, immersing the probe for a couple of minutes to allow sufficient time for equilibration and recording the reading. The probe was rinsed in DDW between samples, and frequently re-calibrated using pH 7 and pH 9 standard buffer solutions at 20°C (this combination of buffers was appropriate since their pH values were within 2 units of all sample readings). Erroneous pH

measurements can arise from high temperature and high photosynthesis rates resulting in carbon dioxide depletion causing brief periods of very high pH in lakes (Moss *et al.*, 2003). If pH readings appeared erroneous, water samples were taken from a different location (avoiding plant beds) and the analysis repeated.

Electrical Conductivity (EC)

Based on the principle that the purer the water the greater the resistance to electrical current, specific conductivity measurements give an indication of the total quantity of dissolved inorganic solids present in a sample (Mackereth *et al.*, 1978). In bicarbonate-dominated lakes specific conductance is closely proportional to the concentrations of the major cations, Ca^{2+}, Mg^{2+}, Na^{+}, K^{+} (Wetzel & Likens, 2000). Electrical conductivity (EC) was measured in the field using a hand-held 'Hanna™ HI 9033' multi-range (0-1999 μScm^{-1}) conductivity meter. To obtain measurements the probe was placed directly in the reservoir, just below the water surface. Alternatively, if excessive wave action prevented stabilisation of the conductivity reading, measurements were taken in a large beaker of reservoir water sample.

Secchi depth (SD)

Secchi depth (SD) is a widely used measure of the transparency of the water, bearing an approximate relationship to the depth of the euphotic zone (euphotic depth (Z_{eu}) = 1.7 SD) (Moss, 1998a, p.206). SD varies seasonally and spatially as a result of algal population fluxes and loadings of inorganic particles (Morris & Fan, 1998). It was measured in the field on each sampling occasion (if access to sufficiently deep water was possible) in each reservoir by lowering a weighted, 20 cm diameter Secchi disc into the water and recording the depth at which the black and white portions were no longer distinguishable to an observer at the water surface (Tyler, 1968; Wetzel & Likens, 2000). Depth of transparency is largely independent of surface light intensity but becomes erratic near dawn and dusk (Wetzel & Likens, 2000). Sampling avoided these times, but it was logistically impossible to make all measurements at the optimal time of midday.

Water temperature (Temp)

The greatest source of heat in water is solar irradiance by direct absorption. Surface water temperature was measured in the field using a wet-bulb thermometer and recorded in °C.

Other field notes

Other observations at the time of sampling were recorded in a field notebook. Notes included observations such as the time of day; weather conditions (air temperature, wind

strength and direction, sun / cloud cover); depth of water in the reservoir and the presence of algal blooms. These observations were recorded to provide at a later date, possible explanations for any idiosyncrasies in the seasonal environmental and species datasets.

Analytical methods employed in the laboratory

Alkalinity (Alk)

Alkalinity in water is a measure of the carbonate-bicarbonate-carbon dioxide equilibrium which is primarily responsible for the buffering capacity of a lake, that is, its ability to receive H^+ or OH^- ions without changing its pH. Alkalinity was measured on unfiltered water samples in the laboratory. This followed Method A (HMSO, 1981) suitable for determination of alkalinity over the range most frequently encountered in water samples i.e. 20-1000 mgl^{-1} as $CaCO_3$. Since only a couple of sites showed low alkalinities in the range 0-20 mgl^{-1}, it was not deemed appropriate to carry out further analyses on only a few samples using the more accurate Gran titration (Gran, 1952). Additionally no samples were highly coloured and thus the above method was considered suitable. For alkalinity determination 100±5 ml of sample (V ml) was pipetted into a 250 ml conical flask. Since all but one site showed alkalinities in the range 20 – 200 mgl^{-1} $CaCO_3$, a 0.02N hydrochloric acid (HCl) solution was used for titration. Phenolphthalein was used as the visual indicator at pH 8.3 (colour change pink to colourless) and this end point represented the titration of all hydroxide and half the carbonate present (T_3 ml). The end point at pH 4.5 was detected visually using bromocresol green-methyl red indicator (colour change greenish blue to grey/pink) and represented the total alkalinity of the sample (T_4 ml). A blank determination was also carried out (T_5 ml) along with a determination of the normality of the 0.02N HCl solution (N_2). Total alkalinity in the range 20-200 mgl^{-1} $CaCO_3$ was calculated using the following formula:

$$=SUM(T_4–T_5)* N_2*(50050/V) \qquad mgl^{-1} \text{ as } CaCO_3$$

Cations and anions: Ca^{2+}, Mg^{2+}, Na^+, K^+ and Cl^-

Concentrations of the major cations and anions were determined only once during the sampling period (on water samples collected in January 2000), due to the relatively low seasonal variation shown by these variables (Wetzel & Likens, 2000). The cations, Ca^{2+} and Mg^{2+} were measured following the methods described in Ebdon *et al.* (1998). Analyses were performed using a Varian 600 AA Spectrophotometer (range 0-1 mgl^{-1}). Dilutions of mainly 1:100 were required. The cations, Na^+ and K^+ were measured using a Digital Corning Clinical Flame Photometer 410C. Water samples were aspirated into a low

temperature flame and the discrete frequency of excitation energy emitted by the Na^+ and K^+ atoms on cooling was isolated by the appropriate optical filter for each cation. A high concentration working standard (10 mgl^{-1}) and a blank (0 mgl^{-1}) were run periodically to calibrate the instrument and to check for drift. Concentrations were determined by comparison with standard curves prepared using the known calibration standards. Dilutions of up to 1:4 were necessary for samples with high concentrations of Na^+. The anion, Cl^- was measured using a "Technicon Autoanalyser II" system and associated "Bran+Luebbe AACE 5.0" computer software, following Method G-133-95 Rev.1 (multitest MT8). This automated procedure for the determination of chloride depends on the liberation of thiocyanate ions from mercuric thiocyanate by the formation of un-ionized, but soluble, mercuric chloride. In the presence of the ferric ion, the liberated thiocyanate forms a highly coloured ferric thiocyanate in proportion to the original chloride concentration. This is compared spectrophotometrically to standards of known concentration. The method is sensitive in the range 0-20 mgl^{-1} Cl^- and most samples required dilutions in the ratio 1:3.

Total Oxidised Nitrogen (TON)

Nitrogen is widely recognised as a key nutrient. TON i.e. nitrate (plus nitrite) represents a measure of the inorganic form of nitrogen biologically available for plant growth. TON analysis was performed on filtered samples in the laboratory. The method was automated using a "Technicon Autoanalyser II" system and associated "Bran+Luebbe AACE 5.0" computer software. TON was measured according to Method 328-86E rev.A, which is based on the coupling of N-1-napthylethylene diamine dihydrochloride and the diazo compound formed in the reaction between nitrite and sulphanilamide. The product was a reddish-purple azo-dye which could be measured spectrophotometrically at 520 nm. TON was measured by the reduction of nitrate to nitrite by a copper-hydrazine reducing reagent. The resulting nitrite then completed the reaction discussed above. This was compared to standards of known concentration. The method was sensitive in the range 0–0.5 mgl^{-1} TON and most samples were diluted between 1:10 and 1:20.

Total Nitrogen (TN)

TN includes both inorganic and organic nitrogen, the latter of which may be equally as abundant and is sometimes easily mineralised for growth by algae and plants. Unfiltered water samples were used for analysis of TN in the laboratory. The method used to determine TN concentration was developed by Mr. Kevin Solman (Senior Technician in the Department of Geographical Sciences at the University of Plymouth), based on the method of Nydahl (1978), and adapted for the equipment available at the University of Plymouth.

5.0 ml of oxidising solution (13.52 g di-potassium peroxodisulphate ($K_2S_2O_8$) and 100 ml 1.5M sodium hydroxide (NaOH) diluted to 1 litre with deionised distilled water) was added to 5.0 ml of sample in a 15 ml pyrex culture tube. The tube was immediately covered with a Teflon-lined screw-top cap and placed in an autoclave at 120°C for 30 minutes. Following oxidation, the solution was cooled to room temperature and the digested samples analysed for TON on a "Technicon Autoanalyser II" system and associated "Bran+Luebbe AACE 5.0" computer software using the same method (328-86E) and with the same sensitivities as described for TON analysis. The dilution factor due to the addition of oxidising solution was accounted for when calculating TN.

Soluble ('Filterable') Reactive Phosphorus / Ortho-phosphate (SRP)

Phosphorus is of key importance in lake ecology (OECD, 1982). SRP is a measure of the biologically available form of phosphorus. Analysis was carried out on filtered samples in the laboratory and automated using a "Technicon Autoanalyser II" system and associated "Bran+Luebbe AACE 5.0" computer software. SRP was measured according to Method 410-89E, which is based on the reduction of a phosphomolybdic heteropolyacid in an acidic solution to the molybdenum blue complex by the action of ascorbic acid. The reaction is sensitised by the use of antimony potassium tartrate. The molybdenum blue compound is measured spectrophotometrically at 880 nm, this being a more sensitive wavelength (when antimony potassium tartrate is used), than the 660 nm of the blue colour. This was compared to standards of known concentration. The method is sensitive in the range 0.005–0.5 mgl^{-1} P.

Total Phosphorus (TP)

TP includes both inorganic and organic phosphorus. Unfiltered water samples were used for analysis for TP. Organic phosphorus requires an acid environment for oxidation of the P into SRP. This method used to determine TP concentration was developed by Mr. Kevin Solman (Senior Technician in the Department of Geographical Sciences at the University of Plymouth) based on the methods of Murphy & Riley (1962) and Jeffries, Dieken & Jones (1979), but adapted for the equipment available at the University of Plymouth. 0.7ml of oxidising solution (30g di-potassium peroxodisulphate ($K_2S_2O_8$) and 27.5ml concentrated sulphuric acid (H_2SO_4) diluted to 500ml with deionised distilled water) was added to 9.8ml of sample in a 15 ml pyrex culture tube. The tube was immediately covered with a Teflon-lined screw-top cap and placed in an autoclave at 120°C for 30 minutes. Following oxidation, the solution was cooled to room temperature and the digested samples analysed for SRP on a "Technicon Autoanalyser II" system and associated "Bran+Luebbe AACE

5.0" computer software using the same method (410-89E) and with the same sensitivities as employed for SRP analysis. The dilution factor due to the addition of oxidising solution was accounted for when calculating TP.

Dissolved Silica (SiO_2) (Si)

Silica is an important nutrient for diatoms, which exists in solution as either silicic acid (H_4SiO_4) or silicate (SiO_3^{2-}). Below concentrations of approximately 0.5 mgl^{-1} most diatoms lose the ability to reproduce effectively (Lund, 1965). Analysis was performed on filtered samples and automated using a "Technicon Autoanalyser II" system and associated "Bran+Luebbe AACE 5.0" computer software. Silicates were measured following the flow diagram for Method 408-89E, based on the reduction of a silicomolybdic heteropolyacid in an acidic solution to the molybdenum blue complex by the addition of ascorbic acid. Oxalic acid is introduced to the sample before the ascorbic acid to eliminate interference from phosphates. The molybdenum blue colour is measured spectrophotometrically at 660 nm. This is compared to standards of known concentration. The method is applicable over the range 0.002-10.00 mgl^{-1} SiO_2. Samples with levels of SiO_2 above 10 mgl^{-1} required dilution prior to analysis.

Chlorophyll-a (Chla)

In the field a known volume (usually 150 ml) of water was filtered using a Nalgene hand-operated vacuum pump, and the filtrate collected on a 0.45 μm pore size Whatman™ WCN cellulose nitrate membrane filter. The filter paper was folded in half with its inner surfaces coming together, placed into a graduated sterile tube, 1ml of magnesium carbonate ($MgCO_3$) added as a preservative and the tube capped and refrigerated in the dark at 4°C prior to pigment extraction in the laboratory. Although it is now widely accepted that the most accurate means of quantifying chloropigments and carotenoids is by high-performance (ion-pairing) liquid chromatography (HPLC) (Wetzel & Likens, 2000), the equipment is expensive and the technique time-consuming. Instead, the methods of pigment extraction and measurement from Golterman *et al.* (1978) and Wetzel & Likens (2000) were adopted. Initial trials were carried out to determine whether rupturing of the algal cells was necessary. Results suggested that grinding significantly increased the extraction of pigments, thus a mortar and pestle was used to grind the filter papers to increase the efficiency of acetone extraction. In May 1999, three replicate samples were analysed from selected sites. Results indicated that there was minimal within-site variability and thus single samples from each site were deemed sufficiently representative during subsequent sampling sessions.

Chla concentrations were calculated, after first subtracting the absorbance at 750 nm from the absorbance at 663 nm (A_{663}) to correct for the presence of fine colloidal matter. The following function was used:

$$=SUM((11.0*(A_{663}*volume))/Vd) \qquad \mu gl^{-1} \text{ Chla}$$

Where:

volume = volume of acetone in mls (i.e. 10)
V = volume of water filtered (in litres)
d = path length of the spectrophotometer cell in cms (i.e. 1)

3.3.2 Modern diatoms – collection and preparation

Plankton

Diatom plankton samples were collected seasonally from each reservoir to enable determination of the seasonal dynamics of different planktonic diatom taxa in different reservoirs. Samples were collected from the epilimnion (at approximately 0.5 m below the water surface) in 1 litre, screw-top polyethylene bottles. To prevent sample deterioration, 100 ml of methanol was added to each sample and thoroughly mixed. Once transported back to the laboratory, samples were allowed to settle in the dark overnight. The overlying water was siphoned off using a suction pump, and the residue homogenised and poured into 250 ml glass beakers and topped up with DDW. This was left to settle overnight and again, the overlying water was removed, taking care not to siphon off any sedimented material.

Preparation of plankton samples for diatom analysis broadly follows the methods described in Battarbee *et al.* (2001). Approximately 50 ml of 30% hydrogen peroxide (H_2O_2) was added to the samples which were then placed on a hot plate at 90°C in a fume cupboard until frothing had subsided and all organic matter had been digested. Care was taken to prevent the samples boiling dry. A few drops of 10% hydrochloric acid (HCl) were added to neutralise the H_2O_2, and the samples removed from the heat. Once cooled in the fume cupboard, all samples were topped up with distilled, deionised water (DDW) and allowed to settle overnight. The following day, all samples were siphoned, topped up with DDW and left to settle again. This washing process was repeated 3-4 times. Although this process was time consuming, it avoided the need to centrifuge samples and thus reduced the likelihood of valve breakage. Samples were then diluted as necessary to achieve a solution with a pale, 'milky' appearance (sample dilution noted). A few drops of 10% HCl were added to increase the ionic concentration of the solution, to reduce clumping and improve dispersal of diatoms on the finished slides. Well mixed sub-samples of diatom suspension were then

pipetted volumetrically (subsample volume recorded) onto 19 mm diameter coverslips. These were left to evaporate on a light-box in a dust and air current-free environment for one to two days. Finally the coverslips were mounted onto glass microscope slides in a few drops of Naphrax ™ high refractive index mountant and placed on a hotplate in a fume-cupboard at 130°C to drive off the toluene in the Naphrax ™.

As noted by Round (1998), counting of acid-cleaned modern diatom samples may introduce error to the delineation of diatom habitat preferences since contamination of the plankton by dead and live cells from other habitats can occur. Ideally ecological studies should be based on observations of live material. However floras based on internal cell morphologies are rare and those that do exist (e.g. Cox, 1996) are not comprehensive for the taxa encountered in the current study. In particular, delineation of small centric diatom taxa would have been particularly difficult from live material, thus the use of acid-cleaned material was considered the preferred option for the identification of contemporary diatom assemblages to species level.

Other diatom habitats

Samples of diatoms from other habitats were collected qualitatively during various seasons to enable delineation of taxa found in the surface sediments and core sequences to their respective preferred habitats. This was considered useful for ecological interpretation. The methods employed for collection, preservation and preparation of epilithic, epiphytic, epipelic and epipsammic diatoms broadly follow those described by Battarbee *et al.* (2001).

3.3.3 Surface sediment sampling

Surface sediment samples were taken primarily during the final fieldwork session in September and October 2000, coinciding with the final water sample collection and theoretically comprising diatom remains laid down throughout the preceding eighteen months in response to the ambient environmental conditions over the same time period. A number of reservoirs were also sampled for surface sediment during earlier fieldwork sessions with the aim of determining seasonal variability in the sedimentation of diatom remains, and hence the influence of sampling strategy on the results of surface sediment diatom analyses. For a few reservoirs surface sediment samples taken in June 2000 were used because sediment sampling was not possible in September / October 2000 (see Appendix 2 for details).

Short cores were retrieved from a boat, anchored in the deepest, least disturbed location at each of the 46 reservoirs using a modified gravity Glew-type corer (Glew, 1989; Glew *et al.*, 2001). The Glew corer was used as it is specifically designed to minimise down-core disturbance of the sediments and to preserve the sediment-water interface intact for subsequent sub-sampling. The uppermost 2 cm of each core was extruded in the field using an extruding bung and rod. The sediment was sliced at the following intervals: 0-0.5 cm, 1.5-1 cm and 1-2 cm and placed into labelled Whirlpak™ polythene bags. Since 20-40 cm cores were often obtained, further sediment samples were retained at many sites to enable examination of the diatoms in these older sediments for evidence of dissolution and hence potential for longer term palaeo-studies at a later date. Sediment samples were stored in a portable refrigerator whilst in the field and then transferred to the cold store on return to prevent dessication and microbial growth. A dated list of all surface sediment samples collected, along with notes on sample depth, Munsell soil colour of the wet surface sediment and any other interesting sedimentary features is provided in Appendix 2.

3.3.4 Sediment cores

Core collection and subsampling

Long sediment cores were collected from both Blackbrook and Daventry reservoirs. The core from Daventry (DAV00F) was extracted in April / May 2000 using a modified Glew-type corer (Glew, 1989; Glew *et al.*, 2001). This core was collected and sub-sampled by Dr. Warren Eastwood and colleagues from the University of Birmingham as part of a research project for Daventry District Council. Other cores were also collected at the same time, including DAV00A and DAV00G. DAV00F was used for diatom analysis and ^{137}Cs dating. DAV00A, taken in a similar location to DAV00F, was used for lithostratigraphic analyses. DAV00G, the master core was used for geochemical analyses and ^{210}Pb and ^{137}Cs dating. The core from Blackbrook (BBK00C) was collected on 28th June 2000 using a 52 mm diameter Mackereth corer (Mackereth, 1969). This core was collected specifically for the current study by a team from the University of Plymouth and all results presented from Blackbrook reservoir relate to this core. BBK00C was extruded in the laboratory and sliced at 0.5 cm vertical intervals to a depth of 10 cm and subsequently at intervals of 1 cm to the core base. The sediment cores from Blackbrook and Daventry are discussed in further detail in Chapter 8, where coring locations are also illustrated.

Lithostratigraphic analyses

Percentage dry weight (%DW), organic matter (%LOI) and carbonate content (%CO_3) of sub-samples from the sediment slices taken from cores BBK00C and DAV00A were

determined following the methods of Dean (1974). The %DW of each level was calculated by weighing approximately 1 g (mass recorded to nearest 1 x 10^{-4} g) of homogenised wet sediment in a pre-weighed crucible (a), which was then immediately re-weighed (b). The sediment was then dried in an oven at 105°C for 24 hours and then re-weighed (c). Percentage dry mass was estimated using equation 1 below. %LOI was subsequently determined by placing the crucible containing dried sample in a muffle furnace at 550°C for two hours. Samples were allowed to cool to room temperature in a dessicator, re-weighed (d) and %LOI estimated using equation 2 below. Subsequently, the same samples were placed in the muffle furnace at 950°C and ignited for a further two hours and re-weighed (e) to give the percentage carbonates (%CO_3), estimated using equation 3 below. Both equations 2 and 3 express the results as percentages of dry mass. The ratio of organic matter to carbon varies considerably for different sediments. To obtain the approximate amount of calcium carbonate ($CaCO_3$), the % loss at 950°C was divided by 0.44 (Dean, 1974).

Equation 1:	% DW	=SUM(((c-a)/(b-a))(100))
Equation 2:	% LOI	=SUM(100-(((d-a)/(c-a))(100))
Equation 3:	% $CaCO_3$	=SUM(((d-e)/0.44))/(d-a))(100))

3.3.5 Dating of sediment cores

Sediment cores must be accurately dated to determine the timing of important stratigraphic changes. The most widely used methods for dating cores over timescales relevant to reservoir eutrophication (i.e. the last 100 - 200 years) are the lead-210 (^{210}Pb) and caesium-137 (^{137}Cs) methods (Appleby, 2001). ^{210}Pb is a naturally occurring radionuclide that is removed from the atmosphere by precipitation or dry deposition, accumulating in soils and sediments. Where succeeding layers of sediment are buried by later deposits, the fallout of ^{210}Pb incorporated into the sediments reduces exponentially with time in accordance with the radioactive decay law. With a half-life of 22.28 years, ^{210}Pb is ideally suited to date sediments laid down in the last 100-150 years. The CRS (constant rate of ^{210}Pb supply) model is the most widely used dating model (Appleby, 2001); it assumes a constant rate of supply of ^{210}Pb from the atmosphere, through the water column and into the sediments, irrespective of sediment accumulation rates. However if there are interruptions in the ^{210}Pb supply, for example changes in the normal pattern of sediment focussing, or hiatuses in the sediment record, then the CIC (constant initial concentration) model or a composite model may be more appropriate.

^{137}Cs is an artificial radionuclide. Fallout on a global scale began in 1954 following the onset of atmospheric nuclear weapons testing, reached a peak in 1963 shortly after the test-ban treaty and then declined steadily until the Chernobyl reactor fire in 1986. Where there is a good qualitative record of atmospheric fallout, sediments recording these events can be identified and thus dated, providing an independent chronological sequence and thus an independent dating technique (Appleby, 2001).

Dr. Stuart Black at the University of Reading provided dates for the sediment cores collected from Daventry reservoir. Numerous samples from the master core DAV00G were analysed for both ^{137}Cs and ^{210}Pb. ^{210}Pb dates were determined using the CRS model (Appleby & Oldfield, 1978; Robbins, 1978). DAV00F (the core used for diatom stratigraphic analyses) was also dated, but solely using the ^{137}Cs method. The ^{210}Pb chronology obtained for core DAV00G was compared with the ^{137}Cs dates from both cores to provide an independent chronological validation of the ^{137}Cs dates derived for core DAV00F. Results are discussed in full detail in Chapter 8.

3.3.6 Preparation of diatom slides from sediment samples

Surface sediment samples

The 0.5-1.0 cm surface sediment sample from each reservoir (October 2000 or in some reservoirs, June 2000) was prepared for diatom analysis. The reasoning behind selection of the 0.5-1 cm sample is discussed in Chapter 6.

Samples were prepared for diatom analysis using wet sediment weighed to mass approximately 0.3 g (exact mass recorded), with subsequent treatment following the methods described for diatom plankton samples.

Sediment core samples

26 levels from BBK00C (Blackbrook reservoir) and 17 levels from DAV00F (Daventry reservoir) were prepared for diatom analysis, following the methods described for both plankton and surface sediment samples. However, to enable more accurate quantitative diatom estimates a known volume of exotic polystyrene markers (microspheres) in solution (concentration 5.44×10^6 spheres ml^{-1}) was added to the diatom suspensions after the final washing stage and homogenised completely before mounting (Battarbee & Kneen, 1982). This enabled the calculation of diatom cell concentrations in each sediment sample using the equations detailed in Battarbee & Kneen (1982) (see section 3.6.3) and hence accurate

estimates of changes in diatom productivity over time in both Blackbrook and Daventry reservoirs.

3.4 Diatom analysis

3.4.1 Diatom identification and taxonomy

Diatoms were identified to species or sub-species level using phase contrast and an oil immersion objective under x1000 magnification using either an Olympus BX-50 or an Olympus BH-2 light microscope (LM). The Olympus BX-50 microscope with accompanying image analysis system (Analysis™) was utilised to aid detailed diatom morphometric analysis and the capturing of images to CD for future reference.

A JEOL JSM-5600 LV scanning electron microscope (SEM) was employed to further aid the identification and delineation of predominantly small and medium-sized centric diatom taxa. All SEM work was carried out in the SEM Unit at the University of Plymouth under the guidance of Dr. Roy Moate and Peter Bond. Concentrated sample suspensions were pipetted onto stubs, dried under a mercury vapour lamp and then sputter-coated with gold. Stubs were examined under an electron beam acceleration voltage of 15kV, a spot size of 10-20 mm and a working distance of between 10-15 mm. Images were saved to CD for future reference.

Principal floras used in identification were Hustedt (1930-1966) and Krammer & Lange-Bertalot (1986, 1988, 1991a, 1991b). Numerous taxonomic papers were also consulted, aiding principally with the identification of planktonic, centric taxa. Papers consulted included, i) for *Aulacoseira* spp. identifications, Haworth (1988), Canter & Haworth (1991), Krammer (1991a,b), Le Cohu (1996) and Siver & Kling (1997); ii) *Stephanodiscus* spp., *Cyclostephanos* spp. and *Cyclotella* spp. identifications, Stoermer & Håkansson (1984), Håkansson & Hickel (1986), Stoermer *et al.* (1987a), Anderson (1990a), Håkansson & Kling (1990), Håkansson & Meyer (1994), Håkansson (2002) and Wolf *et al.* (2002). Taxonomic sessions were also organised with Dr. Elizabeth Haworth (FBA, Windermere), for the delineation of difficult *Aulacoseira* taxa, and with Drs. Carl Sayer and Patrick Rioual (ECRC at UCL), for the determination of troublesome small *Cyclostephanos*, *Stephanodiscus* and *Thalassiosira* species. Appendix 3 provides a list of the dominant diatom taxa, including authorities and codes, for those taxa included in the calibration sets.

Round (1999) comments that taxonomy and ecology are interlocked in that the latter is not possible without the former For most palaeolimnologists however, the autecology of particular species is of the greatest interest - the taxonomy is merely the means to an end. Birks (1994) stresses the importance of taxonomic precision for palaeoenvironmental reconstructions and the need for a sound and detailed taxonomy. However, Stoermer (2001) highlights the present chaotic state of diatom taxonomy and the difficulties that this presents for researchers. Therefore in the development of the UK lowland reservoir calibration set, considerable attention has been focussed on diatom taxonomic issues, in particular relating to the distinction of (tycho)planktonic taxa that dominate diatom assemblages in these sites.

Centric diatom taxa are frequently found to be a major component of freshwater phytoplankton communities (e.g. Siver & Kling 1997; Reynolds & Irish, 2000; Haworth, 1988). However, some *Aulacoseira*, *Cyclotella*, *Cyclostephanos*, *Stephanodiscus* and *Thalassiosira* species are morphologically similar when viewed in either girdle or valve views alone through the LM at x1000 magnification. Individual taxa can themselves exhibit considerable morphological variation, leading to taxonomic confusion. Hustedt (1930) noted the highly polymorphic nature of valve structure in many species of these genera. In common with the observations of other researchers (e.g. Anderson, 1990a; Bennion, 1993; Sayer, 1997; Siver & Kling, 1997), difficulties were often encountered in the current study whilst identifying and quantifying the centric diatom taxa from UK lowland reservoirs. Critical examination of selected samples under the SEM helped to define distinguishing characteristics, assisting greatly with the analysis of material routinely observed under the LM alone. Exploring the detailed morphological structure of similar species / morphotypes enables the transfer of knowledge from SEM to LM, aiding in the delineation of 'troublesome' taxa. Although the combination of SEM and LM analyses in no way guarantees a successful outcome, it is a useful tool. Appendix 5 provides a synopsis of many of the (tycho)planktonic diatom taxa regularly encountered and identified from the plankton, surface sediments and core material of UK lowland reservoirs. The simultaneous presentation of SEM and LM images provides a valuable identification aid. Difficulties encountered in making taxonomic distinctions are discussed. Greatest attention is focussed on *Aulacoseira* spp., since taxa belonging to this genus were often the most difficult to delineate due to the considerable intraspecific morphological variation exhibited by individual species of the genus.

3.4.2 Counting strategy

At least 400 valves were counted from each surface sediment and core sample. This followed the recommendations of Battarbee *et al.* (2001) and initial test counts carried out in the current study. The following counting strategies were adhered to on encountering broken valves: For araphid pennate taxa, fragments were counted where more than half of the valve was present, although for long pennate taxa where only fragments were regularly seen (e.g. *Synedra ulna* and *Synedra acus*), valve ends were counted as half valves. Specifically for fragments of *Asterionella formosa*, only the largest of the two different sized bulbous valve ends were counted. Fragments of raphid taxa were counted if the central area containing the raphe endings was present. Centric valves were counted if either the entire central area, or more than half the valve was present.

3.4.3 Determination of diatom cell concentrations and biovolumes

Diatom cell concentrations

In the current study diatom cell concentrations in seasonal plankton and surface sediment samples were determined using the aliquot method (Battarbee 1986 and Battarbee *et al.*, 2001). Although this is not the recommended method for obtaining quantitative diatom data, it was employed for its ease of application when handling a large number of samples, particularly where diatom cell concentrations were highly variable both between sites and seasons. The following formulae detail the calculations performed for the determination of diatom cell concentrations in plankton, surface sediment and long-core samples. A key to all equations is provided.

Diatom cell concentrations (cells per litre) in modern seasonal plankton samples were calculated using the following formula:

$$=SUM(100*(H/h))*((V/(V/d))*s))/2 \qquad \text{Cells } l^{-1}$$

Diatom cell concentrations (cells g^{-1} DW) in surface sediment samples and long-core samples from DAV00F were calculated using the following formula:

$$=SUM((n*(H/h))*(W/((W/d)*s)))/2)*D \qquad \text{Cells } g^{-1} \text{ DW}$$

Diatom cell concentrations (cells g^{-1} DW) in sediment samples from long-core BBK00C were calculated according to the equations detailed in Battarbee & Kneen (1982) and Battarbee *et al.* (2001), using the following formula:

$$=SUM((((n*M)/m)/W)/2)*D \qquad \text{Cells } g^{-1} \text{ DW}$$

Key to equations

H	= total coverslip area	(mm^2)
h	= proportion of coverslip counted i.e. (FOVs counted * FOV area)	(mm^2)
n	= number of *valves* counted	(no.)
d	= sample dilution	(ml)
V	= sample volume (all samples = 1000 ml)	(ml)
s	= subsample	(ml)
W	= wet weight of sediment	(g)
D	= proportion dry weight (DW) e.g. 20% DW = 0.2	
m	= number of microspheres counted	(no.)
M	= number of microspheres in sample (435,200 in each sample)	(no.)

Diatom biovolumes

As cell size varies considerably between species, biovolume provides a potentially more reliable indication of cell carbon content (and hence biomass) than cell concentrations (Reynolds, 1984). Biovolumes of individual diatom taxa encountered in the current study from both seasonal plankton samples, surface sediment samples and sediment core samples are listed in Appendix 4 and were estimated using one of the following methods:

- Diatom cell dimensions measured under both LM and SEM (e.g height and radius for centric diatoms; height, major semi-axis and minor semi-axis for most pennate diatoms) were entered into the computer programme, BIOVOL (Kirschtel, 1996; available for download at www.msu.edu/~kirschte/biovol). Biovolumes were calculated using formulae specific to the shape of the diatom taxon concerned. In the absence of reliable height estimates, centric diatom cell volumes were estimated using the assumption that the height of each cell was approximately half its diameter i.e. its radius (cf. Bailey-Watts *et al.*, 1989b). The height of a pennate diatom taxon was assumed to be equal to the length of its minor semi-axis.
- In the absence of *any* primary measurement data, biovolumes were either calculated in BIOVOL using average published cell dimension measurements taken from Krammer & Lange-Bertalot (1986, 1988, 1991a, 1991b), or alternatively were assigned according to published values (e.g. The Academy of Natural Sciences, 2001).

3.4.4 Display of diatom data

Distribution of diatom data along environmental gradients

Surface sediment diatom data are expressed as percentage relative abundance. The program CALIBRATE version 0.82 (Demo) (Juggins & ter Braak, 1998) was used to plot the distribution of all diatom taxa along selected environmental gradients for the full diatom species dataset. For each taxon, Gaussian response curves were fitted using logistic

regression (ter Braak & Looman, 1986) and weighted averaging (WA) optima were calculated by WA regression and plotted as 'tic' marks.

Stratigraphic plots

Diatom data were entered into Excel spreadsheets. These were saved as WKS-1 files before opening in TILIA version 2.0.b.4 (Grimm, 1991-1993). Stratigraphic plots for the sediment cores BBK00C and DAV00F were displayed using TILIAGRAPH version 2.0.b.5 (Grimm, 1991) using percentage relative abundance data for individual diatom taxa, in addition to total percentages for each habitat group. Total diatom cell concentrations and diatom biovolumes for each sample are also presented alongside diatom inferred reconstructions for the environmental variables TP, Chla and EC. Similar plots were produced for the surface sediment diatom data, with sites ordered according to epilimnetic TP concentrations and species arranged according to derived TP optimas.

Zonation

Using percentage relative abundance data for all individual diatom taxa (no habitat groups), the hierarchical agglomerative clustering method, CONISS, Constrained Incremental Sum of Squares Cluster Analysis (Grimm, 1987), was performed to construct dendrograms from which zones were subsequently determined. The clustering analysis was stratigraphically constrained for the core data but unstratigraphically constrained for the surface sediment data. Resultant assemblage zones were added to the TILIAGRAPH diagrams to aid interpretation and description.

3.5 Statistical techniques employed for data analyses

3.5.1 Calibration set

Environmental data

All water chemistry variables are expressed as mean values over the period January 2000 to October 2000. The reasoning behind this choice of mean period is discussed in detail in Chapter 4. Averages are generally based upon 4 samples (except for the variables Na^+, K^+, Ca^{2+}, Mg^{2+} and Cl^-, where means are based upon 1 sample only per site). SD averages are based on between 1 and 4 samples (mean =3.2). Data for other environmental variables are based on secondary data with only one measurement per site.

Normality in data is a key feature of all parametric statistical tests, including PCA analysis. PCA assumes a linear relationship between variables, and if this assumption is not fulfilled,

then inferences may be subject to error. Consequently, all environmental variables were examined in turn for the extent to which the data corresponded to a normal distribution. Analyses were performed in MINITAB™ Release 13.31 (Minitab Inc™, 2000) using the Anderson-Darling normality test. The results of these tests and the subsequent transformation of data are discussed in detail in Chapter 4. Following the necessary data transformations, the extent of correlation between individual environmental variables was assessed by calculating Pearson's correlation coefficients between pairs of variables in MINITAB™ Release 13.31 (Minitab Inc™, 2000). To enable visual assessment of the relationships between environmental variables, multiple scatterplots were also constructed using CALIBRATE version 0.82 (Demo) (Juggins & ter Braak, 1998).

Author	Area	No. of samples	No. of species (before cut-off)	No. of species (after cut-off)	Cut-off level for inclusion of individual taxa in ordinations (DCA & CCA)
Burgess (current study)	UK lowland reservoirs	46	214	94	≥ 1% relative abundance in ≥ 1 lake and present in ≥ 2
Tibby (2004)	S.E. Australian reservoirs	33	-	118	≥ 1% relative abundance in ≥ 1 sample
Dixit *et al.* (1999)	N.E. USA lakes	257	406	235	≥ 1% relative abundance in ≥ 1 lake and present in ≥ 10
Gregory-Eaves *et al.* (1999)	Alaska, USA	51	465	119	≥ 2% relative abundance in ≥ 1 lake
Siver (1999)	Connecticut lakes, USA	50	40 planktonic	31 planktonic	> 1% relative abundance in ≥ 1 sample and present in ≥ 3
Lotter *et al.* (1998)	Alps, Europe	68	341	64	≥ 20% samples containing the taxa
Hall & Smol (1996)	South-central Ontario (Canada)	54	416	92	≥ 1% relative abundance in ≥ 1 lake and present in ≥ 5
Jones & Juggins (1995)	Antarctic lakes	59	-	83	≥ 0.5% relative abundance in ≥ 1 sample and present in ≥ 2
Wunsam & Schmidt (1995)	Alps and pre-alpine region	86	-	61	> 1% relative abundance in ≥ 3 samples
Bennion (1994)	S.E. England shallow lakes	31	310	102	> 1% relative abundance in ≥ 2 samples
Anderson *et al.* (1993)	Northern Ireland	43	189	112	≥ 1% relative abundance in ≥ 1 sample
Fritz *et al.* (1993b)	Michigan, USA	42	-	98	> 1% relative abundance in ≥ 1 sample
Hall & Smol (1992)	British Columbia	46	-	134	≥ 1% relative abundance in ≥ 1 sample and present in ≥ 2
Dixit *et al.* (1991)	Sudbury (Canada)	72	-	59	≥ 1% relative abundance in ≥ 3 lakes

Table 3.4 Comparison of published cut-off levels with that used in this study, for inclusion of individual taxa in ordinations and inference model construction.

Species data

Two calibration datasets were developed from the surface sediment percentage diatom data and the measured environmental variables. One included all diatom taxa and the other included planktonic taxa only. Lowest predication errors in Weighted averaging (WA) transfer functions may be derived when all diatom taxa are used (Birks, 1998; Cameron *et al.*, 1999; Philibert & Prairie, 2002b). However, in the current study diatom taxa were

included in the calibration datasets if they were present in a minimum of two reservoirs, achieving ≥1% relative abundance in at least one site. This helped to reduce the influence of rare taxa on ordinations. The choice of cut-off was based upon an assessment of cut-off levels used by other researchers in similar studies (see Table 3.4). For the plankton-only calibration dataset and subsequent development of plankton-only inference models, only reservoirs with >50% planktonic diatom taxa in their surface sediment samples were included. Diatom habitat preferences were classified according to the results of modern sampling of seasonal plankton samples examined in the current study and on the basis of published information.

3.5.2 Ordination techniques

Ordination techniques are commonly used to reduce the variation in community composition to the scatter of samples and species in an ordination diagram (ter Braak and Prentice, 1988; Lepš & Šmilauer, 2003). The ordination techniques employed in the current study included Principal Components Analysis (PCA); Detrended Correspondence Analysis (DCA) and Canonical Correspondence Analysis (CCA). All ordinations were performed using the program CANOCO for Windows version 4.0 (ter Braak & Šmilauer, 1998a) and reference manual (ter Braak & Šmilauer, 1998b). All ordination diagrams were plotted using CANODRAW version 3.1 (Šmilauer, 1992a) and CANOPOST version 1.0 (Šmilauer, 1996-7).

Eigenvalues and percentage cumulative variance explained are presented for each ordination analysis. Eigenvalues represent the relative contribution of each component or axis to the explanation of the total variation in the data. The size of the eigenvalue indicates the importance of the axis in explaining the variation in the dataset (Kent & Coker, 1992). In a sample ordination, the cumulative percentage variance is a measure of how much variation in the species data is explained along the axes of the ordination.

The use of ordination techniques provided an objective way in which to examine calibration set environmental and species data to subsequently identify and eliminate extraneous data typical of large ecological data sets. The data screening process in the current study involved removing:

a) 'Outlier' samples with particularly unusual environmental characteristics and/or diatom assemblages (identified through PCA and DCA ordinations respectively).
b) Environmental variables that had little or no influence on diatom distributions (identified through CCA).

c) Redundancies in environmental information, such as variables that were correlated among lakes but did not independently influence diatom distributions (identified through PCA and CCA).

Principal Components Analysis (PCA)

The indirect gradient analysis technique of Principal Components Analysis (PCA) was performed to detect the major environmental gradients in the 46-reservoir calibration set and to identify outlier sites displaying extreme or unusual environmental characteristics. If a site had >1 environmental variable with extreme (>x5 standard deviations) influence (i.e. high 'leverage') it was considered for removal (Birks *et al.*, 1990).

PCA was performed on a correlation matrix, with centring and standardisation of the environmental data. The analysis was initially carried out with all 46 sites and 26 environmental variables included.

Detrended Correspondence Analysis (DCA)

Detrended Correspondence Analysis (DCA) (Hill, 1979) is an indirect gradient analysis technique where species distributions are explored independent of environmental data (Hill & Gauch 1980). Since DCA assumes a unimodal distribution of taxa along an environmental gradient, it overcomes distortion problems such as the 'arch' effect (Kent & Wathern, 1980) and the 'horseshoe' effect (Gauch & Whittaker, 1981) associated with linear methods and 'sparse' data matrices. Consequently DCA is generally considered superior to linear techniques (i.e. PCA and RA) for the indirect ordination of species data (see Kent & Coker, 1992 for a discussion). In the current study DCA was utilised to reveal major patterns of variation in both the surface sediment and seasonal plankton diatom species data.

The DCA analyses employed in the current study were performed on percentage diatom data using the default options available in CANOCO version 4.0, namely detrending by segments and nonlinear rescaling, with no species transformations (ter Braak & Šmilauer, 1998). Rare taxa (i.e. taxa with percentage abundances less than one fifth of the most common taxon) were down-weighted in proportion to their frequency (Hill & Gauch, 1980; ter Braak & Šmilauer, 1998b). DCA gradient lengths of >3 standard deviation (SD) units indicate that most species responses can be approximated by unimodal response models (Jongman *et al.*, 1995). Økland (1990) suggests that DCA is able to recognise the gradient structure even with compositional turnover rates as low as 2 SD units. In the current study

gradient lengths of 2-3 SD units have been taken to indicate suitability for the application of unimodal direct gradient analysis techniques e.g. CCA / DCCA.

Canonical Correspondence Analysis (CCA)

Canonical correspondence analysis (CCA) (ter Braak 1986, 1994; Palmer 1993; Jongman *et al.*, 1995) is a direct gradient analysis technique that can be applied when associated species and environmental data are available. CCA assumes a unimodal relationship between species and environmental variables and is therefore an appropriate ordination method to employ if DCA of the species data indicates long species gradients. CCA constrains an ordination of one matrix (sites and species) by a multiple linear regression on variables in a second matrix (sites and environmental variables) (McCune & Grace, 2002). It ignores community structure that is unrelated to the environmental variables and is therefore utilised to assess the statistical significance of species-environment relationships. This enables the determination of those environmental factors most strongly correlated with species distributions, thus demonstrating potential for the development of inference models.

The literature on the process of selection of environmental variables for inclusion or exclusion in CCA is extremely unclear, and as a result remains an essentially subjective process (Kent, 2001a). ter Braak & Šmilauer (1998b) recommend that a small number of carefully selected variables is preferable to the inclusion of a large number of poorly chosen ones. Large ecological datasets contain redundancies in environmental information, unusual samples and environmental variables that do not determine diatom distributions (Hall & Smol, 1992). Prior to the implementation of CCA, PCA and DCA analyses were employed to screen the environmental and species datasets respectively. Outlying sites showing unusual environmental characteristics and / or atypical species assemblages were removed. CCA was then employed to identify a subset of environmental variables that explained both significant ($P \leq 0.05$) and partially independent amounts of variation in the diatom data. An identical sequence of techniques was employed on both the full and plankton-only datasets in order to achieve this goal; these are detailed below.

The statistical significance of taxon-environment relationships in CCA was assessed using Monte Carlo permutation tests with 999 random permutations. A Monte Carlo permutation test repeatedly shuffles (permutes) the samples. The null hypothesis states that the species data are unrelated to the environmental data and the alternative hypothesis states that the species respond to the environmental variables. Any variable with $P > 0.05$, did not exhibit a

statistically significant independent influence on diatom distributions and was thus excluded from subsequent analyses.

i. Pearson's correlation matrix

As a first step, the degree of intercorrelation between pairs of measured environmental variables was determined from a Pearson's correlation matrix showing the correlation coefficients and the associated statistical significance of these correlations. Although no environmental variables were removed at this stage, variables showing significant intercorrelation and thus providing no unique contribution to the ordination were highlighted for possible removal following further data pruning exercises.

ii. Constrained CCAs

Secondly, a series of constrained CCAs were run for each environmental variable in turn to establish its ability to explain a statistically significant amount of variance in the species data (ter Braak & Šmilauer, 1998b). The higher the eigenvalue ratio of CCA axis 1 to CCA axis 2 (i.e. λ_1/ λ_2), the greater the importance of the environmental variable in explaining variance in the species data. Variables displaying a low eigenvalue ratio and showing no independent influence over diatom distributions ($P \geq 0.05$, using 999 unrestricted Monte Carlo permutations) were removed from subsequent analyses.

iii. Inter-set correlations

According to ter Braak & Šmilauer (1998b), if the t-value of a variable's canonical coefficient is less than 2.1 in absolute value, then the variable does not contribute much to the fit of the species data in addition to the contributions of the other variables in the analysis. However, since canonical coefficients become unstable when the environmental variables are strongly correlated, it was considered preferable to examine the stable inter-set correlations to determine the significance of correlations between individual environmental variables and CCA ordination axes.

iv. Partially constrained CCAs (pCCAs)

Fourthly, environmental variables capable of explaining significant independent variation in the diatom species data and representing different axes of variation were selected as the sole environmental variables in partially constrained CCAs (pCCAs). The remaining members of each group of correlated variables were entered in turn as covariables to test their ability to independently influence diatom distributions. The statistical significance of taxon-environment relationships (given the covariables) was assessed using Monte Carlo

permutation tests with 999 random permutations. Any variable with $P > 0.05$, did not exhibit a statistically significant independent influence on diatom distributions and was thus excluded from subsequent analyses.

v. Examination of Variance Inflation Factors (VIFs)

The VIF is used by ter Braak & Šmilauer (1998b) to assess the independent contribution of each environmental variable to the overall ordination. If variables have VIFs >20, it is argued that they should be removed from the analysis in turn (largest removed first), until all VIFs <20. Some authors, e.g. Philibert & Prairie (2002a), remove variables until all VIFs are <10. In the current study the variance inflation factors (VIFs) of the remaining environmental variables were examined to identify redundant variables, and those displaying a high degree of colinearity with other variables. Variables with high VIFs were omitted one at a time (largest first), and the CCA rerun until all remaining variables had VIFs <10.

vi. Manual forward selection of environmental variables

Following the above data screening process, a CCA was performed using manual forward selection to identify a subset of environmental variables, where each variable explained a significant proportion of variance in the species data. Manual forward selection is a step-wise process. After testing their statistical significance if they were to be included (using 999 Monte Carlo permutations), environmental variables were selected one after the other for inclusion in the model. A variable only contributed significantly to the model of already included variables if its P value was ≤ 0.05 (tested under).

Variance partitioning

The conditional variance explained by the manually forward-selected environmental variables may not be independent. To further investigate the interaction between measured explanatory variables, variance partitioning (Borcard *et al.*, 1992) was employed. This technique employs canonical ordination (e.g. CCA, RDA) and was applied in the current study to both the full and plankton-only calibration datasets. The percentage of the total variance in diatom assemblages explained by i) individual environmental variables independent of all other measured variables (marginal effects), and ii) the combined effects of two or more variables (conditional effects), were determined. This enabled an evaluation of the unique contribution of individual explanatory variables in addition to an assessment of the degree of interaction between measured covariables. The results are displayed in

Chapter 5 in the form of Venn diagrams, where the areas are approximately proportional to the percentage of variance explained.

3.5.3 Classification techniques

Classification is a process that involves grouping individual samples into classes on the basis of their attributes to look for patterns and order in the dataset (Kent & Coker, 1992). The best classification is one that enables a clear ecological interpretation to be made, where every individual within each group is more similar to the other individuals in that group than to any individual in any other group. Numerical classification by a variety of algorithms (rules defining the process of classification) is used to clarify relationships among sites, species and environmental variables. Although the numerical clustering *methods* themselves avoid subjective bias and give consistent and repeatable results, their interpretation still remains subjective. Zones derived by numerical cluster analysis were also compared with those derived 'by eye' in order to assess their ecological logic.

All cluster analyses performed in the current study using contemporary species and environment data were carried out using the program PC-Ord version 4.0 (McCune & Mefford, 1999) under guidance from Kent (2001b). Cluster analyses were performed to a) classify sites with respect to their environmental characteristics; b) classify sites with respect to their species assemblages; c) classify sites with respect to both environmental and species characteristics.

For the environmental data, similarity analysis was performed using the hierarchical agglomerative Ward's method of minimum variance clustering (Ward, 1963), which uses the squared Euclidian distance dissimilarity coefficient. The environmental dataset consisted of a large number of variables and was thus 'noisy'. To overcome this problem, clustering was performed on the PCA axis scores (for the first two or three axes) as opposed to the raw data values. This generated superior clusters because the information afforded by the large number of individual variables was combined into components (axis scores) corresponding to the main trends in the dataset. The use of axis scores instead of raw data is justified if the first two or three axes account for a high percentage of variance in the dataset (Everitt *et al.*, 2001).

For the species and species/environment data, Two-Way Indicator Species Analysis (TWINSPAN) (Hill, 1979), a hierarchical divisive method of numerical cluster analysis was performed. This is the preferred and most widely used method of numerical classification

for species data since it was written specifically for the analysis of species data and can thus cope with sparse data matrices (Kent & Coker, 1992).

3.5.4 Inference model development (Calibration)

The computer program C^2 Version 1.3 (unlicensed version; Juggins, 2003a) with its associated user guide and tutorial (Juggins, 2003b,c) was employed to generate diatom-based inference models from the UK lowland reservoirs full and plankton-only calibration sets.

Models were developed for the inference of single environmental variables (TP, Chla and EC), using weighted averaging regression and calibration (ter Braak & van Dam, 1989), both with (WA_{tol}) and without (WA) tolerance downweighting and executed using both inverse and classical deshrinking. Models based on partial least squares (PLS) and weighted averaging partial least squares (WAPLS; ter Braak & Juggins, 1993) were also developed and the performance statistics of all models compared. In addition, models created using square-root transformed species data were compared with those employing untransformed data and the influence of removing outlier sites and species was assessed for each model. These procedures are discussed in full in Chapter 7.

Paralleling the use of an independent test set, realistic error estimates were derived from estimation of the root mean squared error of prediction (RMSEP). In each case this was estimated using leave-one-out jack-knifing cross-validation, in which each sample is removed in turn from the dataset before sample DI-values are predicted from its diatom flora (ter Braak & Juggins, 1993; Birks, 1998). The average bias in prediction errors and the maximum average bias in 10 equally divided segments of the environmental gradient are also estimated by jack-knifing to enable assessment of systematic differences between inferred and measured values (Birks, 1998). The residuals associated with each model were also plotted to determine the presence of bias in model predictions.

The theory behind tolerance downweighting, bootstrap-derived estimates of prediction of error, and deshrinking techniques are discussed in detail by ter Braak & van Dam (1989) and Birks *et al.* (1990).

3.5.5 Application of inference models for environmental reconstructions

The inference models developed were used to perform WA calibration and hence environmental reconstructions on fossil diatom data from the long cores BBK00C and

DAV00F. Bootstrap cross-validation was performed to obtain sample-specific standard errors for each fossil sample. Full details are given in Chapter 8.

3.5.6 Reconstructions using the European Diatom Database (EDDI)

Although TP reconstructions for cores BBK00C and DAV00F were performed using the inference models developed in the current study, reconstructions using the European Diatom Database Initiative (EDDI) Combined TP training set (Juggins *et al.*, 2001) were also performed to provide comparative results. The EDDI Combined TP model is based on 345 sites and 477 taxa (range of TP is 2-1189 μgl^{-1} - mean is 99 μgl^{-1}) and is a dataset based on the amalgamation and harmonisation of nine regional calibration sets. The EDDI User Guide version 1.0 (Juggins, 2001) was consulted to aid reconstructions using EDDI. The fossil diatom data was harmonised with that in the EDDI Combined TP training set. This ensured that the taxon codes and taxonomic concepts applied to the codes in the cores matched those used in the EDDI Combined TP dataset. The fossil data file was converted from an Excel spreadsheet into Cornell condensed format using the program WinTran version 1.0 beta (Juggins, 1998). This file was then uploaded onto the EDDI server and a TP reconstruction performed on-line using locally-weighted weighted averaging (LWWA). LWWA dynamically generates a 'local' calibration set for each fossil sample based on the 50 closest analogs defined by the minimum chi-squared distance. This is the recommended method of reconstruction for large merged datasets because it outperforms traditional WA and WAPLS methods due to its ability to cope with the additional noise which can be introduced as taxonomic diversity and environmental gradients increase (Juggins, 2001). Results were downloaded and TP reconstruction trends compared with those derived using the models developed in the current study. A full discussion is provided in Chapter 8.

PART THREE

Results

CHAPTER FOUR

Synthesis of the reservoir calibration set environmental data

4.1 Introduction

This chapter provides a synthesis of the environmental data. The ranges and statistical distributions of measured chemical and physical variables are described and relationships between them investigated, with data presented in both tabulated and graphical form. This chapter seeks to draw out patterns in the environmental dataset, observe correlations between variables and define environmental gradients through the use of ordination techniques (i.e. Principal Components Analysis (PCA)). The data presented, analysed and discussed in this chapter are carried forward to Chapter 6 for input into direct gradient analyses (i.e. Canonical Correspondence Analysis (CCA)) in association with the species data that is presented in Chapter 5.

4.2 The nature of the environmental data

The full chemistry dataset consists of seven seasonal samples from 46 reservoirs, spanning an 18-month period including two summer seasons (May 1999 – October 2000).

Water chemistry variables, particularly those nutrients used or produced by algae, often demonstrate marked seasonal variation and the impact upon subsequent analyses of utilising mean data sampled over different time periods needs to be considered. The 18-month dataset comprises more summer / autumn samples than winter / spring samples. Thus mean values calculated over this period would be expected to over-estimate the mean values of variables that attain peak values over the summer / autumn months e.g. chlorophyll-*a* (Chla). Conversely, variables such as dissolved silica (Si) and total oxidised nitrogen (TON) would be under-represented as they usually attain their highest values in the unproductive winter months. Mean data calculated from environmental measurements taken in different seasons over a reservoir's annual cycle, would be expected to provide more representative 'annual' mean values. However, by reducing the dataset to cover only an annual period, some information is lost and mean values must be derived from fewer individual samples. Nonetheless, this was considered the most ecologically sound option in the current study and all subsequent analyses employ annual mean values for all water chemistry variables, except chlorophyll-*a* maximum (ChlaM) and secchi depth minimum (SD_{min}) whose maximum and minimum respectively over the full 18-month sampling period were employed. 'Annual' periods do not actually comprise data spanning a full 12-month period,

however they comprise samples taken in different months reflecting the four seasons and thus constitute representative 'annual' mean values.

Table 4.1 illustrates that for the environmental dataset collected in this study there were three possible 'annual' periods and one 18-month period over which seasonally determined variables could be averaged. The period selected to provide representative data was M3 (January 2000 – October 2000). This decision was based on the results of individual Mann-Whitney non-parametric statistical tests, which were performed to determine whether the differences observed between seasonal environmental data averaged over different periods were statistically significant. Mean environmental data for the ten seasonally measured variables from each combination of periods M1-M4 was used in these analyses. At the 95% confidence level, results indicated that overall there was no significant difference between data averaged over any of the different periods. The only significant differences were seen for Chla, M2 < M4 (P = 0.03), for TON, M1 > M4 (P = 0.03) and for pH, M2 < M3 (P = 0.04). Thus for Chla and TON, M2 and M1 respectively are more similar to the other annual means than to the 18-month mean. The over-representation of summer measurements in the 18-month dataset (M4) is thought to be the source of these differences, thus providing support to an earlier argument for the use of 'annual' mean data. Since there were no significant differences between annual mean values for all variables (except pH, M2 < M3), it was decided to use data for M3 because this period was inclusive of measurements taken at the time of surface sediment sampling.

Code	M1	M2	M3	M4
Samples encompassed by each period over which the seasonally measured environmental variables were averaged	July 1999 October 1999 January 2000 March 2000	October 1999 January 2000 March 2000 June 2000	January 2000 March 2000 June 2000 September 2000	May 1999 July 1999 October 1999 January 2000 March 2000 June 2000 September 2000

Table 4.1 Samples encompassed by the different periods (M1 – M4) over which the seasonally measured environmental variables were averaged. The period selected - M3 - is shaded. Please see text for reasoning.

Numerous authors (e.g. Birks, 1998; Bennion & Smith, 2000) stress the importance of high quality environmental data to provide representative annual averages for the generation of predictive models. Intra-annual variability for many water quality variables can be high and tends to be greatest in the most nutrient enriched waters (Gibson *et al.*, 1996; Bennion & Smith, 2000). Thus, a high sampling frequency is usually necessary to define representative

annual mean data, and the more eutrophic a lake, the more samples may be required. Gibson *et al.* (1996) and Bradshaw *et al.* (2002) demonstrated that annual maximum total phosphorus (TP) was highly correlated with the range and mean TP, but less so with the minima. The same holds true for the dataset in this study (Figure 4.1). Thus TP, and other nutrient, estimates may be inaccurate when based on only a few measurements. Although the sampling protocol in this study cannot by any means be termed 'high frequency', it does attempt to account for broad seasonal variation in a systematic way.

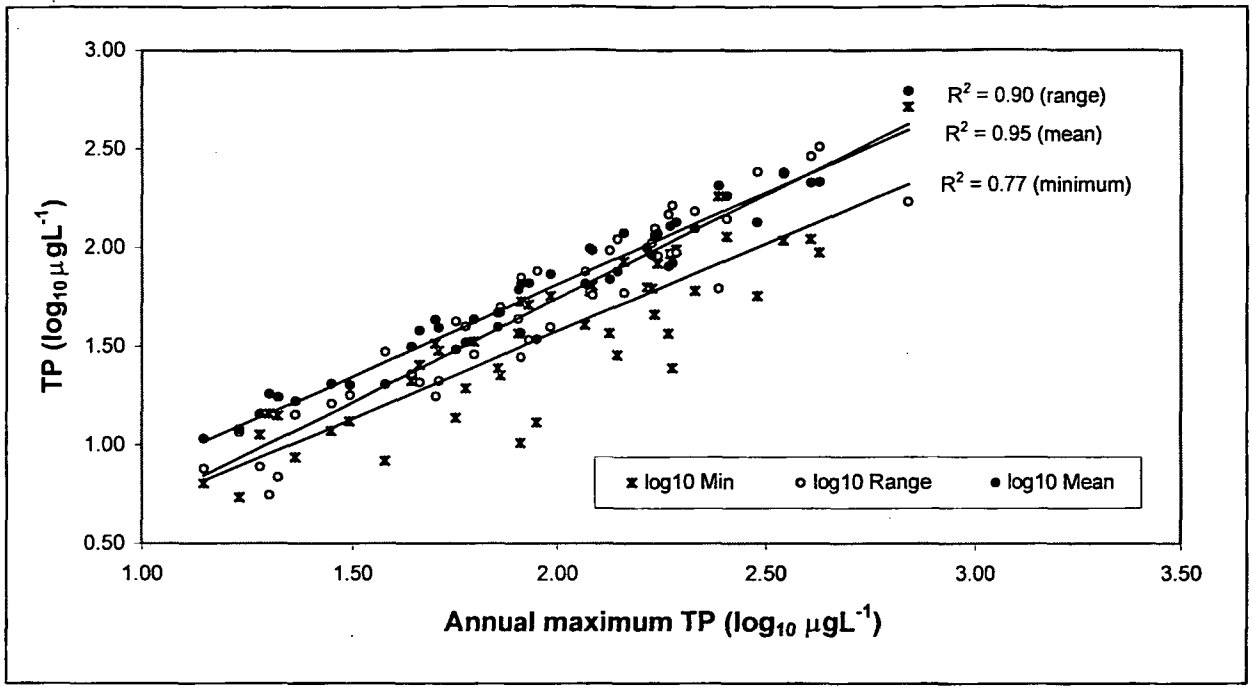


Figure 4.1 Measured annual maximum TP concentration plotted against minimum, mean and range for the 46-reservoir dataset.

An improvement might entail utilising data for selected variables based on higher frequency sampling, such as that carried out by individual Water Companies. When the mean values in this study derived from low frequency sampling are compared to those from selected reservoirs obtained from high frequency sampling by water companies, there is often little difference for variables such as pH where intra-annual variability is inherently low. However, differences do become more apparent for highly dynamic variables such as nutrients. Figure 4.2 clearly illustrates this point, using site 7 (Chew Valley) as an example. The graph displays the high frequency soluble reactive phosphorus (SRP) data supplied by Bristol Water Works (small circles and line) alongside the seasonal measurements taken in this study (large diamonds). The water company data provide detailed information on both intra- and inter-annual variability in SRP, illustrating the cyclical seasonality of this variable. The data collected in this study provide highly comparable values to the Water

Company data for each seasonal sample, but fail to capture the more short-lived, but pronounced trends seen at certain times of the year, which only continuous monitoring can detect. As a result, the 12-month mean value, calculated from low frequency sampling (113 μgl^{-1}) is significantly different to that calculated from the high frequency data (177 μgl^{-1}). This discrepancy results from this study's sampling programme consistently missing the late summer peak in SRP and hence underestimating the annual average SRP concentration. This demonstrates the inevitable compromise in terms of data quality / consistency and sampling logistics in a study of this nature.

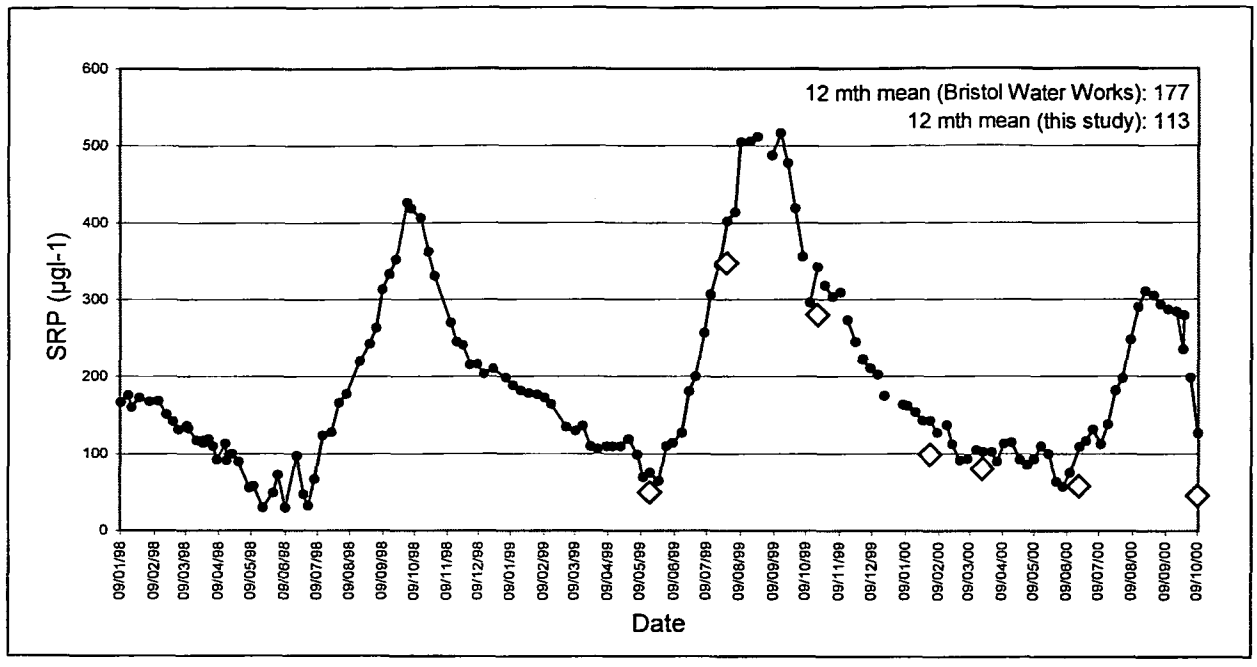


Figure 4.2 **Illustration of inter- and intra-annual variation in SRP concentrations, and comparison of the ability of high versus low frequency sampling regimes to capture nutrient seasonality and provide representative annual mean data for SRP in Chew Valley Reservoir (site 7). High frequency sampling data (line and small symbols) courtesy of Bristol Water Works, low frequency data (open diamonds) from this study.**

Issues relating to prediction are also important. Anderson *et al.* (1993), Tibby (2004) and Bradshaw *et al.* (2002) test hypotheses about which models (e.g. annual average, winter maximum or spring minimum, TP) provide the best diatom inferred TP (DI-TP) model. This approach has ecological relevance, acknowledging that in many lakes, the main growth periods for planktonic diatoms occur in the early spring and autumn, and thus diatom-nutrient calibration datasets could be improved by using winter maximum or spring minimum TP measurements, as opposed to annual average values. However, in sites with year-round phytoplankton growth, mean annual TP may provide the best model. Both Tibby (2004) and Bradshaw *et al.* (2002) conclude that DI-TP models based on mean annual

values perform best. Although this may not necessarily hold true in the current study, it does go some way towards supporting the use of mean annual values in model generation, particularly since the temporal resolution of sampling in the current study is considered insufficient for the calculation of representative seasonal averages.

4.3 Ranges and statistical distribution of environmental variables

4.3.1 Summary statistics

Summary statistics (means, medians, minima, maxima and standard deviations) for the 16 water chemistry variables and 10 site characteristics are reported in Table 4.2. Table 4.3 displays the 16 measured water chemistry variables, together with SD_{min} and TN:TP ratio data, on a site-by-site basis to illustrate inter-site variation.

Water quality variables are expressed as mean values calculated for the most part from 4 seasonal samples collected from each of the 46 sites over the period between January and September 2000. However:

a) for the variables sodium (Na^+), potassium (K^+), calcium (Ca^{2+}), magnesium (Mg^{2+}) and chloride (Cl^-), data are based on only 1 winter sample from each site;

Environmental variable	Acronym	Units	No. of samples	Mean	Median	Min	Max	St.Dev
pH	pH	pH	4	7.93	7.97	6.40	9.72	0.57
Alkalinity	Alk	mgl^{-1}	4	91.00	86.00	4.00	239.00	53.00
Conductivity	EC	μScm^{-1}	3	419.00	422.00	100.00	942.00	186.00
Na^+	Na	mgl^{-1}	1	13.98	11.95	4.80	36.00	7.96
K^+	K	mgl^{-1}	1	3.90	3.75	0.70	8.80	1.83
Ca^{2+}	Ca	mgl^{-1}	1	13.70	11.16	0.25	55.57	9.79
Mg^{2+}	Mg	mgl^{-1}	1	4.23	2.85	0.18	13.83	3.43
Cl^-	Cl	mgl^{-1}	1	33.41	26.11	12.27	98.34	17.32
SiO_2-Si	Si	mgl^{-1}	4	3.45	3.23	0.00	13.51	2.43
TON	TON	mgl^{-1}	4	3.01	2.38	0.00	9.75	2.19
TN	TN	mgl^{-1}	4	4.25	4.00	0.73	14.42	2.18
SRP	SRP	μgl^{-1}	4	48.00	11.00	0.00	650.00	93.00
TP	TP	μgl^{-1}	4	90.00	57.00	5.00	691.00	109.00
Chlorophyll-*a* (mean)	Chla	μgl^{-1}	4	6.70	3.90	0.00	46.30	8.10
Chlorophyll-*a* (maximum)	ChlaM	μgl^{-1}	7	19.95	14.37	4.10	90.71	17.10
Secchi depth	SD	cm	2 - 4	254.00	214.00	50.00	800.00	126.00
Water depth (mean)	Z_{mean}	m	-	5.71	5.55	2.60	12.60	1.56
Water depth (maximum)	Z_{max}	m	-	15.20	14.00	5.00	35.00	7.00
Volume	Vol	Ml	-	9646	2837	120	124000	20190
Age	Age	years	-	59.33	45.50	21.00	196.00	38.77
Altitude	Alt	m.a.O.D	-	93.87	85.00	0.00	240.00	62.04
Catchment area	Cat	km^2	-	18.88	12.10	0.00	109.30	22.08
% Agriculture in catchment	Agri	%	-	64.49	75.00	0.00	95.00	28.77
Reservoir type	Type	0,1,2 or 3	-	-	-	-	-	-
Geology	Geol	1,2 or 3	-	-	-	-	-	-
Destratification	Destrat	yes / no	-	-	-	-	-	-

Table 4.2: Summary statistics for the 26 measured environmental variables at the 46 calibration set sites.

Site No.	Site Code	pH	Alk mgl^{-1}	EC μScm^{-1}	Na mgl^{-1}	K mgl^{-1}	Cl mgl^{-1}	Ca mgl^{-1}	Mg mgl^{-1}	Si mgl^{-1}	TON mgl^{-1}	TN mgl^{-1}	SRP μgl^{-1}	TP μgl^{-1}	Chla μgl^{-1}	ChlaM μgl^{-1}	SD m	SD_{min} m	TN:TP ratio
1	ARD	8.20	118	781	34.8	6.4	71.5	20.1	7.5	2.2	4.2	6.2	9	43	6	11	2.01	1.50	144
2	BBK	7.85	110	460	14.4	4.6	37.5	8.6	9.7	4.1	2.7	6.4	76	118	6	26	2.08	1.20	54
3	BLA	8.44	170	473	8.3	3.7	18.2	15.3	6.0	3.5	1.7	3.3	69	126	14	37	2.20	1.30	26
4	BLI	8.10	105	449	10.9	6.5	25.2	14.5	8.8	6.4	3.8	4.9	80	119	6	18	2.50	1.40	41
5	CHD	8.04	140	406	5.3	1.8	14.5	11.2	1.1	2.2	3.3	4.3	6	17	4	13	5.50	4.00	245
6	CHL	7.64	77	371	10.8	2.8	24.6	3.9	2.5	4.2	4.6	5.6	162	216	2	23	1.53	1.00	26
7	CHW	8.59	163	468	8.8	3.7	18.5	11.9	4.5	1.8	1.4	2.2	71	129	7	19	3.80	1.00	17
8	CLA	7.38	20	119	4.8	1.4	25.8	4.9	2.3	2.1	2.4	4.2	7	17	4	6	4.67	2.30	250
9	COS	8.08	207	773	18.8	4.0	51.8	34.0	1.2	8.1	7.0	8.6	109	184	5	38	1.73	0.75	47
10	CRO	8.02	96	415	13.6	3.2	35.3	7.0	6.3	3.9	1.6	3.1	36	69	7	91	2.37	0.40	45
11	DRA	8.41	106	666	24.6	6.9	52.8	18.1	8.6	3.0	2.0	3.1	59	99	4	10	3.70	2.40	32
12	DUR	8.39	122	434	8.7	3.5	21.2	12.4	6.1	2.6	4.3	6.2	21	96	26	75	0.56	0.35	65
13	EYE	8.10	111	536	13.8	3.5	37.6	20.8	4.6	2.6	4.2	6.3	9	31	2	5	2.82	1.75	199
14	FOR	8.26	136	607	18.0	5.1	37.9	25.1	6.8	4.6	3.9	5.1	165	206	3	5	4.13	3.00	25
15	FOX	8.19	93	408	9.2	2.3	24.4	9.2	2.8	2.8	1.3	2.4	12	38	4	20	2.05	1.50	64
16	GRA	8.57	187	887	36.0	8.8	66.4	55.6	4.3	4.0	5.2	6.7	549	625	5	14	2.47	1.60	11
17	HAW	8.29	127	387	6.8	1.2	17.4	7.1	5.0	3.0	3.2	4.3	11	21	7	12	2.87	2.60	210
18	HOL	8.14	80	384	8.8	4.1	22.9	9.2	2.2	1.3	2.3	4.0	3	33	9	25	1.83	1.00	122
19	LEI	8.46	35	179	6.4	1.3	17.2	6.2	2.0	4.2	2.3	3.7	3	14	5	13	4.05	2.10	256
20	LUX	8.08	68	284	6.5	1.4	18.4	17.2	2.1	7.7	2.2	3.1	12	34	5	9	1.90	1.20	91
21	NAN	8.33	121	483	10.0	3.0	32.7	8.8	13.8	5.1	2.7	5.2	9	65	12	37	1.07	0.45	79
22	OGS	7.94	79	378	12.6	3.8	26.4	7.7	2.6	4.2	3.0	4.0	19	47	5	8	3.18	1.85	85
23	PIT	8.03	98	488	14.6	4.6	37.3	14.2	3.4	2.0	3.6	5.1	15	30	2	7	4.23	3.30	169
24	POR	7.71	49	292	14.6	3.5	36.9	0.3	3.3	4.9	4.9	5.9	9	39	9	21	1.13	0.70	150
25	RAV	8.13	90	410	8.1	2.8	25.3	9.4	1.9	1.8	4.8	6.2	2	20	7	15	2.90	1.50	309
26	RUT	8.20	118	644	28.8	7.0	58.7	29.5	5.1	2.2	3.5	5.0	29	76	3	7	3.07	1.20	65
27	STA	8.16	126	539	13.2	5.2	40.5	21.3	3.3	4.1	3.8	5.0	21	66	8	24	1.88	0.80	76
28	STN	8.09	142	649	19.8	6.0	42.9	24.3	11.0	3.3	3.5	5.0	70	135	3	13	2.47	1.35	37
29	STI	6.98	11	129	8.7	2.3	21.9	3.2	7.4	0.4	1.8	2.6	4	18	5	8	3.40	1.60	144
30	SUT	7.96	151	431	8.5	3.6	20.3	14.5	0.9	3.6	2.4	3.7	16	73	17	35	0.78	0.50	51
31	SWI	8.39	113	503	13.4	3.8	36.2	11.2	12.5	5.9	1.5	2.9	68	135	12	42	3.10	1.00	21
32	THO	8.28	125	584	25.2	5.6	57.7	14.4	11.3	3.7	2.2	3.8	41	99	13	31	1.60	1.40	39
33	TIT	7.08	35	197	8.2	4.2	20.0	6.7	0.4	4.5	1.9	3.1	9	43	2	6	2.08	1.60	73
34	TRE	6.65	7	110	6.5	0.7	16.5	3.3	1.4	4.3	2.2	2.7	5	11	2	5	4.70	4.00	248
35	TRI	7.64	78	372	10.2	3.2	23.9	21.0	2.9	4.2	4.6	5.5	158	215	3	17	1.65	1.10	26
36	UPT	7.15	22	183	8.8	3.0	22.4	5.0	0.9	1.7	3.4	5.0	8	61	14	26	1.08	0.70	81
37	WIM	7.16	23	139	5.0	1.5	12.3	7.6	0.2	1.8	2.9	3.2	3	12	3	4	6.17	4.00	269
38	WIS	7.64	32	141	5.8	1.1	14.6	8.3	2.7	1.5	2.0	2.6	2	20	7	12	3.53	2.40	126
39	ARG	7.49	46	274	12.4	4.1	24.4	9.9	1.3	2.6	3.1	3.9	3	40	5	7	2.00	1.10	98
40	ARL	8.42	67	419	22.0	6.2	45.3	4.3	2.3	2.3	2.3	3.0	12	66	13	35	1.27	0.75	46
41	BEW	7.64	56	357	16.6	5.1	36.4	25.0	1.6	2.8	2.6	3.1	54	115	4	23	3.27	2.00	27
42	BOU	7.88	78	446	18.4	5.8	40.3	7.4	2.0	3.0	4.2	4.7	149	242	4	8	1.40	1.20	19
43	DAR	7.85	60	342	16.4	3.9	34.0	14.2	1.8	3.6	1.8	2.5	1	81	6	10	1.73	1.15	31
44	POW	7.35	38	349	21.2	2.5	48.1	15.6	2.1	3.3	1.5	1.9	2	37	4	15	1.58	1.00	51
45	WEI	7.47	46	279	11.5	5.1	24.8	10.2	1.1	2.2	2.5	3.0	8	92	6	13	0.97	0.70	33
46	DAV	8.03	121	715	33.2	5.8	98.3	21.3	3.2	6.1	1.8	2.9	3	84	10	21	2.00	0.90	34

Table 4.3: **Eighteen limnological characteristics of the 46 reservoirs – SD_{min} and TN:TP ratio are added as they are discussed later in this chapter. For details of the number of samples from which each mean value is calculated, please see Table 4.2. If means are based on 4 samples, these samples cover the period January – October 2000 (see Table 4.1). For site codes see Appendix 2.**

b) secchi depth (SD) data is based on an irregular number of samples per site;
c) ChlaM data are the maximum value attained over the entire 18-month sampling period in each site;
d) data for seven, site characteristic variables (mean depth (Z_{mean}), maximum depth (Z_{max}), reservoir volume (Vol), reservoir age (Age), altitude (Alt), catchment area (Cat), and percentage agricultural land in catchment (Agri)) are based upon one value / measurement per site;
e) the site characteristic variables, reservoir type (Type), dominant catchment geology (Geol) and destratification (Destrat) are measured on a nominal scale.

The data displayed in Table 4.2 and Table 4.3 illustrate the broad range of values for many variables, reflecting the dynamism of water quality within the dataset. A discussion of these summary statistics will be included in section 4.3.2.

4.3.2 Graphical summary of data

The histograms illustrated in Figures 4.3(a-ac) further display the ranges of environmental variables tabulated in Table 4.2 and Table 4.3 as frequency distributions to enable trends in the dataset to be seen. The class sizes chosen for the variables have been logically assigned according to the data range. Additionally, for variables classified by OECD (1982) to assess the trophic status of freshwater lakes i.e. Chla, SD, SD_{min}, SRP and TP, Figure 4.4 shows the frequency distribution of these variables based on the OECD (1982) class boundaries.

To explore the seasonality of selected environmental variables, box-plots illustrating seasonal data distributions are presented in Figure 4.5(a-l). Box-plots are presented for seven seasons (except Alk for which six seasons are displayed) and illustrate the variation in values over the period May 1999 to September 2000 for all 46 sites. The horizontal line represents the median value, the upper and lower limits of the box represent the upper and lower quartiles, the limits of the bar lines extend to the maximum and minimum points which are within 1.5 times the interquartile range, and the stars indicate extreme values (outliers) outside this range.

The results presented in Figure 4.3(a-ac), Figure 4.4 and Figure 4.5(a-l) interrelate and provide a coherent summary of the environmental dataset. Figure 4.3 (a-ac) presents data relating to variability in *space* among and between the 46 calibration set reservoirs, whereas Figure 4.5 (a-l) presents data relating to variability in *time*. A discussion of the key trends displayed in these figures is presented at the end of this section.

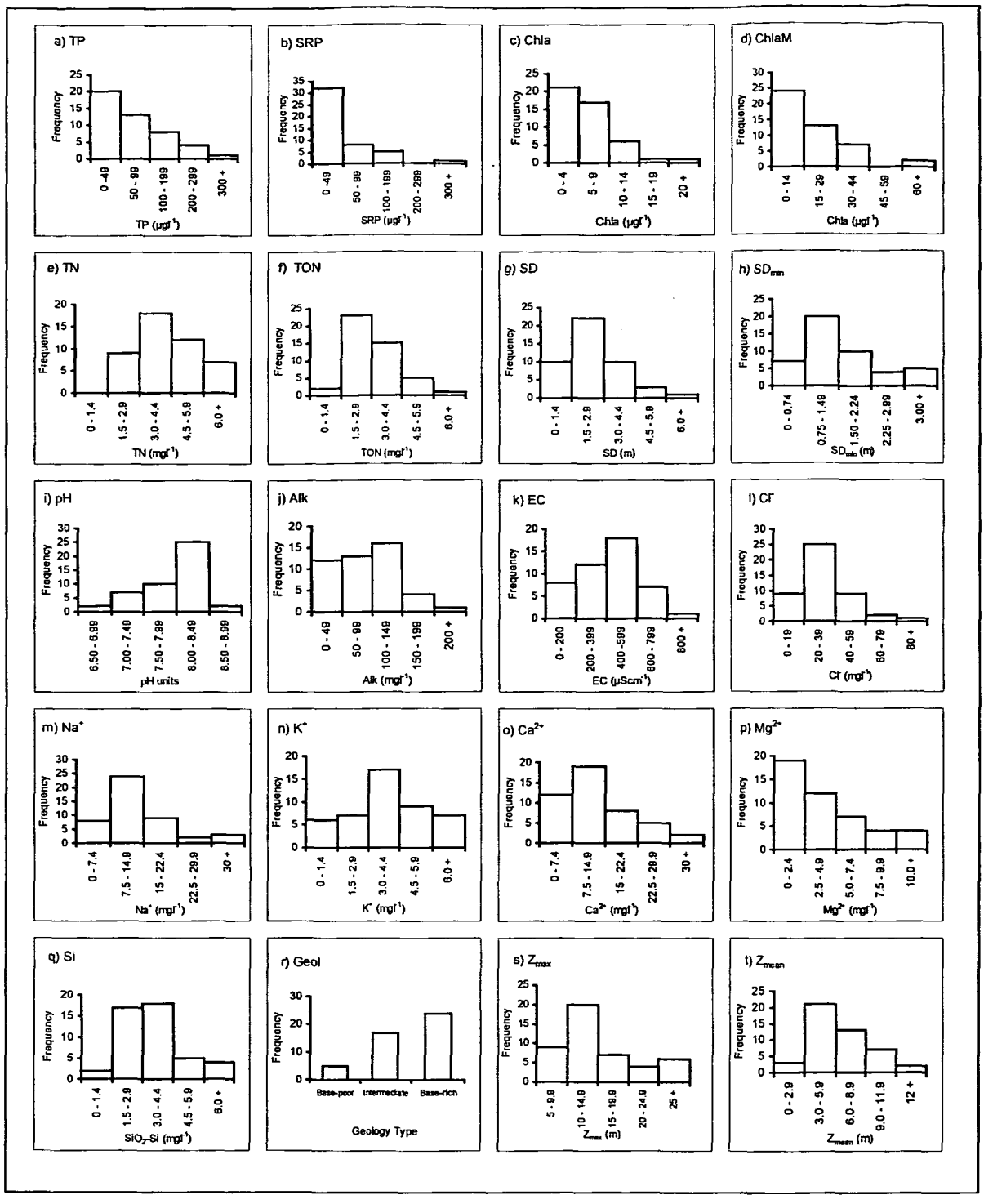


Figure 4.3 (a-t) **Frequency distributions of individual environmental variables (annual mean data) across the 46-reservoir dataset.**

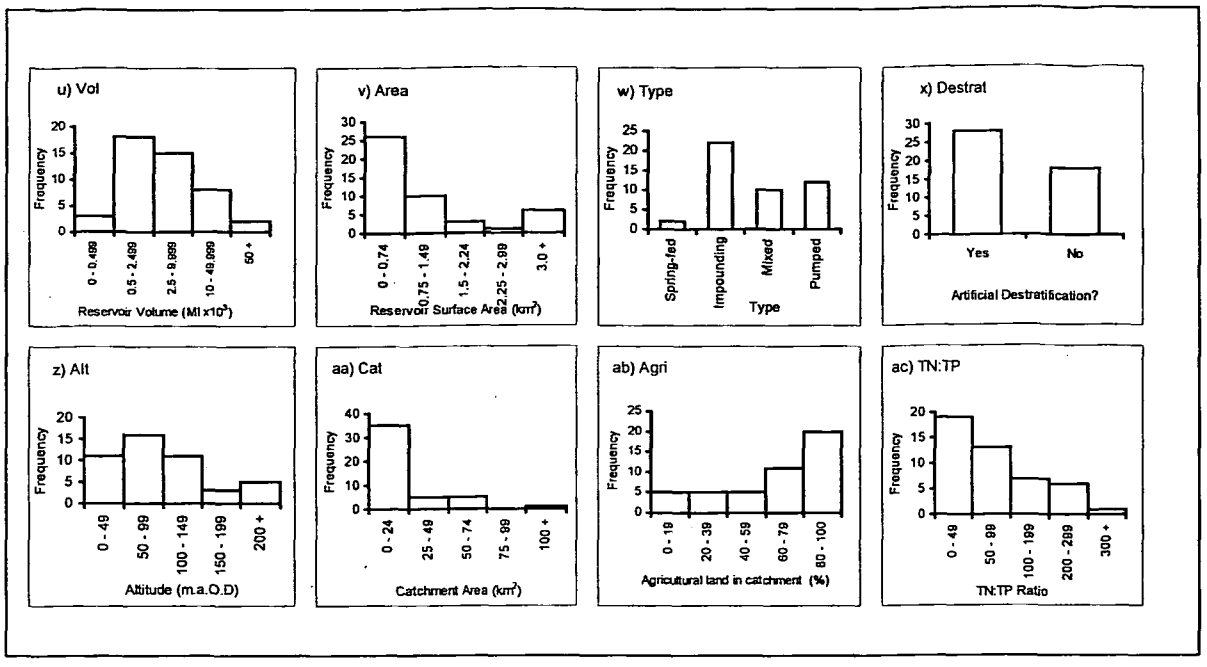
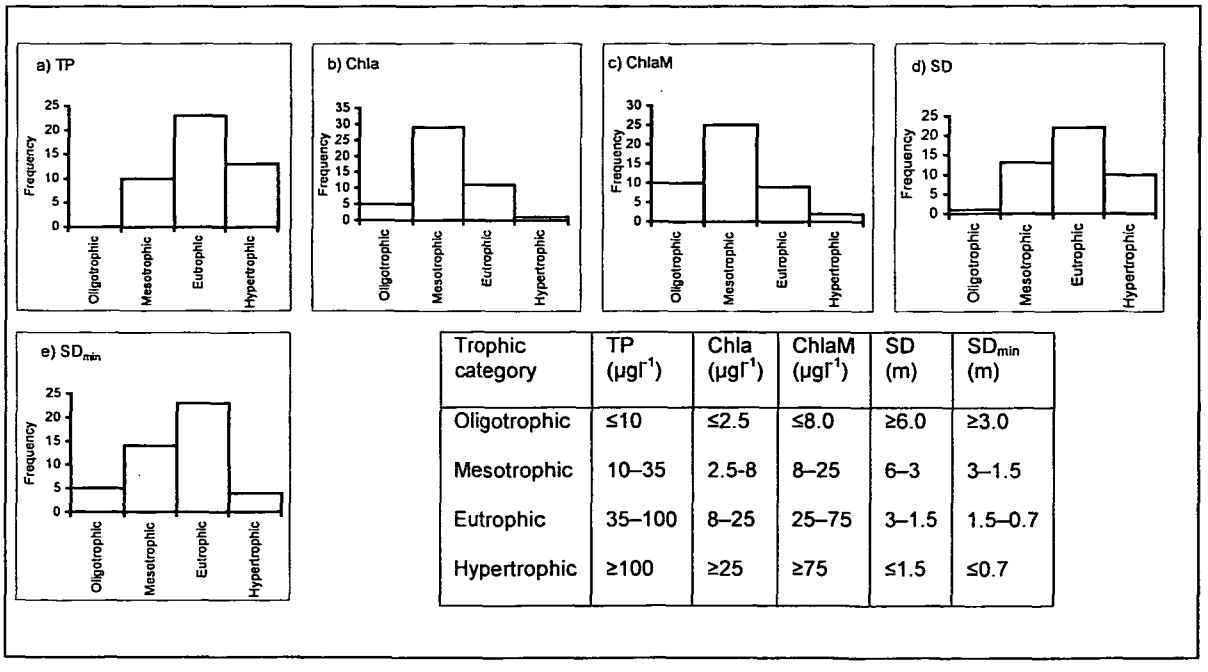


Figure 4.3 (u-ac) **Frequency distributions of individual environmental variables (annual mean data) across the 46-reservoir dataset.**



Trophic category	TP ($\mu g l^{-1}$)	Chla ($\mu g l^{-1}$)	ChlaM ($\mu g l^{-1}$)	SD (m)	SD_{min} (m)
Oligotrophic	≤10	≤2.5	≤8.0	≥6.0	≥3.0
Mesotrophic	10–35	2.5-8	8–25	6–3	3–1.5
Eutrophic	35–100	8–25	25–75	3–1.5	1.5–0.7
Hypertrophic	≥100	≥25	≥75	≤1.5	≤0.7

Figure 4.4 **Frequency distributions of selected environmental variables in the 46-reservoir dataset. Class divisions follow OECD (1982) criteria.**

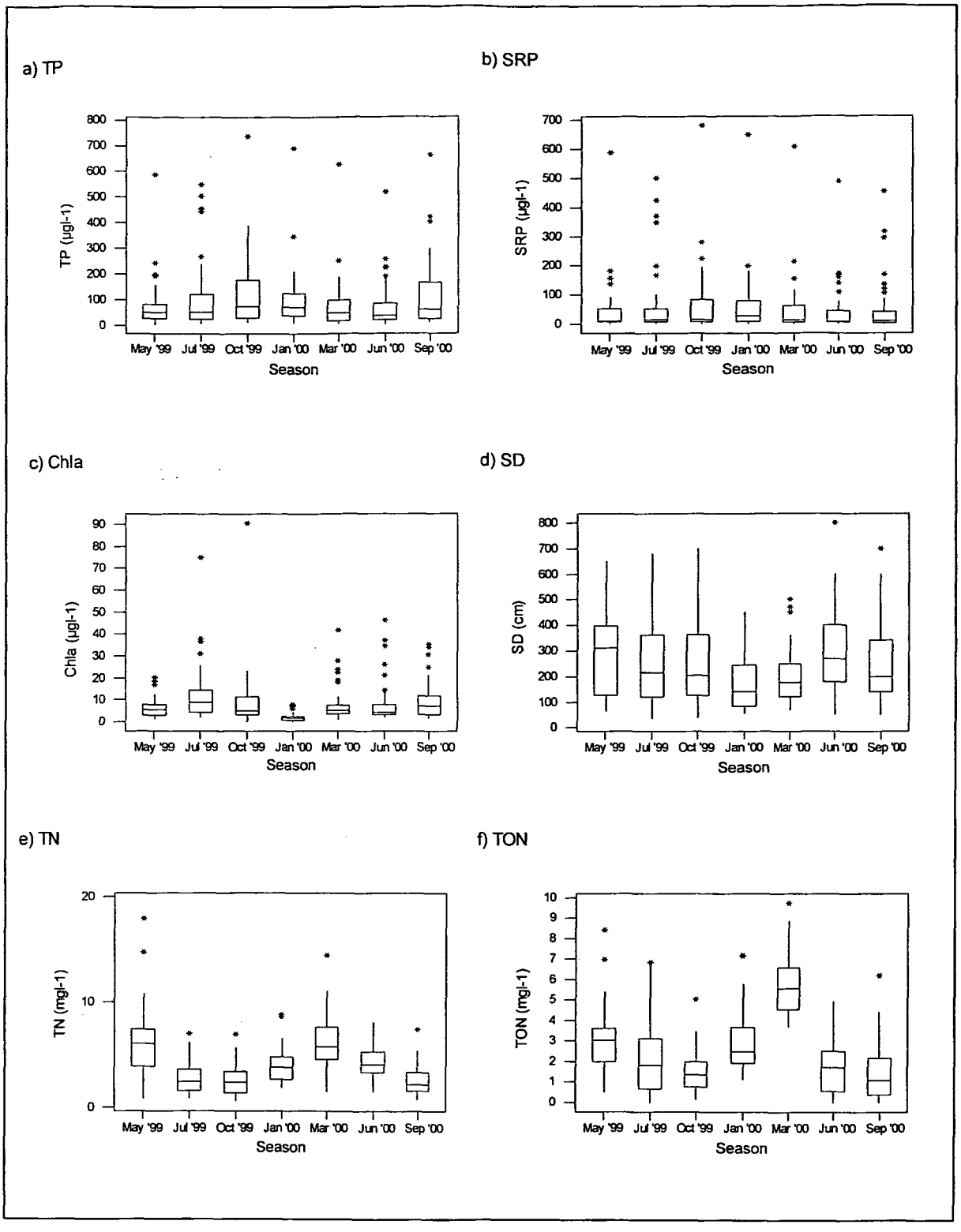


Figure 4.5a-f Box-plots to illustrate a) TP, b) SRP, c) Chla, d) SD, e) TN and f) TON seasonality across the 46-reservoir dataset from May 1999 to September 2000. The horizontal line represents the median value, the upper and lower limits of the box represent the upper and lower quartiles, the limits of the bar lines extend to the maximum and minimum points which are within 1.5 times the interquartile range, and the stars indicate extreme values (outliers) outside this range.

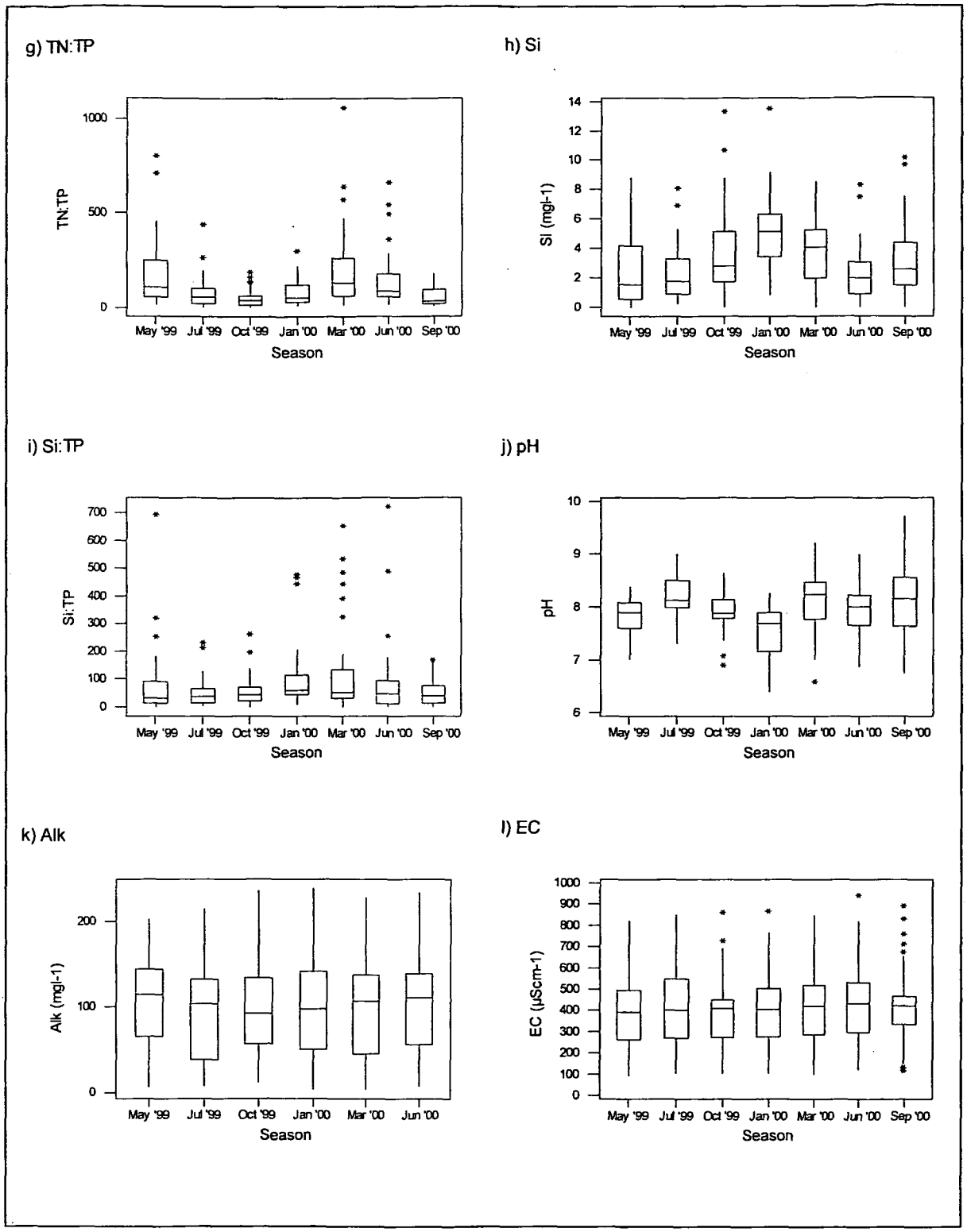


Figure 4.5g-l Box-plots to illustrate g) TN:TP, h) SiO_2-Si, i) Si:TP, j) pH, k) Alk and l) EC seasonality across the 46-reservoir dataset from May 1999 to September 2000 The horizontal line represents the median value, the upper and lower limits of the box represent the upper and lower quartiles, the limits of the bar lines extend to the maximum and minimum points which are within 1.5 times the interquartile range, and the stars indicate extreme values (outliers) outside this range.

Soluble reactive phosphorus (SRP) and Total phosphorus (TP)

Annual mean SRP for the 46 sites ranges from 1 to 549 μgl^{-1} (Table 4.3) with an overall dataset mean of 48 (±93) μgl^{-1}, indicating considerable site-to-site variation (Table 4.2). SRP concentrations have a positively skewed distribution, with most values (approx. 70%) falling in the range 0-50 μgl^{-1}. The remainder of sites have concentrations in the range 50-200 μgl^{-1}, except site 16, which has a concentration of 549 μgl^{-1} (Figure 4.3b).

Annual mean TP for the 46 sites ranges from 11 to 625 μgl^{-1} (Table 4.3) with an overall dataset mean of 90 (±109) μgl^{-1}, indicating considerable between-site variation (Table 4.2). Figure 4.3a illustrates that the frequency distribution of the annual mean TP dataset is positively skewed. Figure 4.4a illustrates that TP concentrations range relatively widely between sites. The majority of reservoirs (50%) have TP concentrations in the range 31-100 μgl^{-1}, and are classed as 'eutrophic' according to OECD (1982) criteria. Thirteen sites (28% of the dataset) can be classed as 'hypertrophic', with TP concentrations greater than 100 μgl^{-1}. The majority of these hypertrophic sites have TP concentrations between 100 and 300 μgl^{-1}, but one clear outlier, site 16, has a TP concentration of 625 μgl^{-1}. Ten sites (22% of the dataset) are classed as mesotrophic (TP 10-35 μgl^{-1}) and there are no reservoirs with mean annual concentrations of TP <10 μgl^{-1}, indicating that none of the sites can be classified as oligotrophic in terms of TP.

The seasonality of TP shows a clear trend. This is characterised by overall high values in the autumn (October 1999 median: 76 μgl^{-1}, September 2000 median: 62 μgl^{-1}) and winter (January 2000 median: 73 μgl^{-1}), with a large range. Values decrease throughout the spring and early summer, with the lowest values recorded in mid-summer (July 1999 median: 52 μgl^{-1} and June 2000 median 37 μgl^{-1}). SRP shows a similar but less pronounced seasonal trend compared to TP, perhaps reflecting its lability and considerable day-to-day variability (cf. Moss *et al.*, 2003). High values prevail in the winter (January 2000 median: 27 μgl^{-1}), with average values less than half this figure throughout the rest of the year, with the lowest mean SRP in June 2000 of 7 μgl^{-1}.

High TP concentrations in the autumn and winter may be attributed to allochthonous P loads entering the reservoirs when suspended particles and soluble forms of P are washed in from diffuse and/or point sources by heavy rains (Carpenter *et al.*, 1998; Bennion & Smith, 2000; Moss *et al.*, 2003). The reservoirs are all located in lowland areas and generally have catchments that lie on easily weatherable sedimentary rocks, thus supporting the observed autumn and winter increases in TP. Internal loading of P, i.e. from allochthonous sources,

can also increase in the autumn and winter when strong winds cause mixing and resuspension of particulate P from the sediments into the water column (e.g. Boström *et al.*, 1982; Søndergaard *et al.*, 1992; Bennion & Smith, 2000; Moss *et al.*, 2003). Associated increases in SRP concentrations may be seen in the autumn and winter, but at lower absolute values than TP. Although most of the P entering the reservoirs at this time arrives in particulate form and contributes to the observed increases in TP, some P arrives in soluble form (SRP), most likely from direct run-off of agricultural fertilisers from the surrounding catchment. Low concentrations of both SRP and TP in the spring and summer are generally attributed to the rapid assimilation of the biologically available phosphorus (SRP) in early spring, when increased light and temperature favour phytoplankton growth (Reynolds, 1984a). The very low levels of SRP during spring and summer in many reservoirs suggests that across the dataset P is the limiting nutrient (Elser *et al.*, 1990; Guildford & Hecky, 2000).

Total Nitrogen (TN) and Total Oxidised Nitrogen (TON)

Annual mean TN for the 46 sites ranges from 1.9 to 8.6 mgl^{-1} (Table 4.3), with an overall dataset mean of 4.25 (±2.18) mgl^{-1} (Table 4.2). Figure 4.3e illustrates an approximately normal distribution, with the majority (65%) of sites having mean concentrations between 3 and 5.9 mgl^{-1}. Since almost 70% of sites have >60% of their catchment areas under agricultural land-use, the high concentrations of TN are thought to be largely derived from agricultural run-off (Figure 4.3ab). Alternatively, the elevated TN levels could possibly indicate some degree of sewage effluent input.

Annual mean TON for the 46 sites ranges from 1.3 to 7.0 mgl^{-1} (Table 4.3), with an overall dataset mean of 3.01 (±2.19) mgl^{-1} (Table 4.2). The data distribution illustrated in Figure 4.3f is more positively skewed than that displayed for TN, with 50% of sites having concentrations between 1.5 and 3.0 mgl^{-1}. These concentrations are relatively high and probably indicate that nitrogen is not the limiting nutrient in the dataset as a whole. However it is noted that in some sites e.g. Chew Valley reservoir, TON becomes undetectable by mid-summer, which could indicate that N becomes limiting at this time (Moss *et al.*, 1994; James *et al.*, 2003).

Figures 4.5e and 4.5f show that the concentrations of both TON and TN follow a similar seasonal cycle across the dataset, comparable to patterns commonly observed in temperate lakes (Wetzel, 1983; Bennion & Smith, 2000). Most of the sites experience late winter / early spring maxima (January 2000 mean = 3.15 mgl^{-1}; March 2000 mean = 5.87 mgl^{-1}),

followed by decreasing concentrations throughout the summer (May 1999 and July 1999 means = 3.09 and 2.03 mgl^{-1} respectively), with the lowest concentrations experienced in the autumn (October 1999 and September 2000 means = 1.60 and 1.50 mgl^{-1} respectively). According to Bennion & Smith (2000), the seasonal pattern in TON concentrations is similar to that observed for SRP and is attributed to increased rates of assimilation by algae (Reynolds, 1984a) and denitrifying bacteria (Jensen *et al.*, 1992) throughout the spring and summer growing season. It is thought that in the majority of reservoirs sampled in this study the decrease in TON at this time is more attributable to assimilation by algae than denitrification, since most reservoirs are destratified and should not therefore suffer from anaerobic hypolimnia in the summer months, favourable to denitrifying bacteria.

High annual mean concentrations of TON and TN (Table 4.2 and 4.3) may indicate that none of the 46 reservoirs can be considered nitrogen deficient. However, as illustrated above, nitrate concentrations demonstrate a striking seasonal pattern, characterised by peaks and troughs. Barica (1990) stresses the ecological importance of the extreme values in influencing the competitive interactions between different algal groups (e.g. diatoms, chlorophytes and cyanophytes), particularly when they coincide with shifts in relative concentrations of other environmental variables such as phosphorus. Guildford & Hecky (2000) report that N limitation occurs at ratios <9:1 by mass, whereas P limitation occurs at ratios of >22.6. Between these values both N and P could potentially limit phytoplankton growth and a clear relationship between any single nutrient and phytoplankton productivity becomes confounded (James *et al.*, 2003). Figure 4.3ac illustrates the positively skewed frequency distribution of mean annual TN:TP ratios (by mass) in the current study. According to these mean ratios, none of the 46 reservoirs can be classified as N limited and only four sites (Grafham (11:1); Chew (17:1); Swithland (19:1); Bough Beech (21:1)) are considered both N and P limited. Thus according to mean annual TN:TP ratios, the majority of reservoirs are classified as P limited. However, the annual mean TN:TP ratio may be misleading in assessing nutrient limitation (Barica, 1990). The seasonal variability of TN:TP ratios in the 46-reservoir dataset are illustrated in Figure 4.5g, indicating that these ratios are highest in the spring and decrease throughout the summer, to reach the lowest values during the autumn period. These ratios will be discussed further in ensuing chapters, but for the intervening period it is interesting to note the differences in mean values from site to site (Table 4.3). Furthermore, Barica (1990) states that it is the "short-lasting minima of the TN:TP ratios which characterize the nutrient limitation status of a lake" (p.102). When seasonal variations in the TN:TP ratio are tabulated for individual sites (Table 4.4), it

is clear that TN:TP can be highly dynamic in individual lakes, with particularly pronounced minima generally coinciding with the late summer / autumn period.

Season	Year	Site number and name				
		2 Blackbrook	7 Chew Valley	16 Grafham	31 Swithland	32 Thornton
May	1999	85	13	25	105	103
July	1999	31	2	14	19	51
Oct	1999	9	3	3	5	9
Jan	2000	34	16	9	26	40
Mar	2000	143	46	13	81	75
Jun	2000	59	15	14	47	68
Sep	2000	14	4	8	3	11
Mean		54	17	11	21	39

Table 4.4 Seasonality of the TN:TP ratio in selected reservoirs. Shaded boxes indicate periods of N limitation, where TN:TP ratios are ≤ 9:1 by mass.

Chlorophyll-a (Chla) and Maximum Chlorophyll-a (ChlaM)

Annual mean Chla for the 46 sites ranges from 1.8 to 25.5 μgl^{-1} (Table 4.3), with an overall mean of 6.70 (±8.10) μgl^{-1} (Table 4.2). These data show that Chla concentrations vary considerably, indicating wide variations in algal productivity. Figure 4.3c indicates that there is a positive skew in the dataset, with the majority of sites (46%) having mean annual concentrations in the range 0-5.0 μgl^{-1}. Figure 4.4b shows that five reservoirs have mean annual concentrations of Chla ≤2.5 μgl^{-1}, indicating that these sites can be classified as oligotrophic. 24% of sites can be classified as eutrophic and 2% as hypertrophic. Most reservoirs (63%) have Chla concentrations in the range 2.5-8.0 μgl^{-1}, classifying them as mesotrophic. This classification is in disagreement with that based on TP. A possible explanation could be that, although Chla is usually the dominant pigment in algal cells, it is only one of a wide range of algal pigments. If a reservoir is populated by algal species characterised by different pigments, then the Chla concentration may not be wholly representative of a reservoir's phytoplankton productivity. For example, cyanophytes contain phycobiliproteins, pigments specific to the group, alongside other more general algal pigments including Chla, chlorophyll- β, β-carotene and zeaxanthin (Jeffrey *et al.*, 1997). Cyanophytes were noted to produce significant blooms in approximately one third of reservoirs sampled in the current study. Therefore measurements of Chla concentrations in these sites may underestimate total phytoplankton productivity. Alternatively the underestimation of Chla may be an artefact of the sampling protocol, where low frequency sampling has failed to pick up short-lived seasonal chlorophyll maxima in the dataset and hence annual means have been underestimated (see Figure 4.2). A further explanation could be that many reservoirs have a relatively short residence time and thus a comparatively

rapid hydraulic flushing rate. This may decrease the efficiency of transferral of nutrients into algal biomass, thus reservoir Chla concentrations are lower than might be expected from available nutrient concentrations.

Figure 4.5c illustrates that the concentration of Chla follows a marked seasonal cycle. The lowest concentration and range occurs in the winter (January 2000 median: 1.4 μgl^{-1}), concentrations rise during the spring (March 2000 median: 5.1 μgl^{-1}) and early summer (June 2000 median: 4.0 μgl^{-1}), to peak in the late summer / early autumn (July 1999 median: 8.9 μgl^{-1}, September 2000 median: 7.2 μgl^{-1}). The ranges increase as the summer progresses, indicating that some of the sites were experiencing much greater algal productivity than others.

Annual mean ChlaM for the 46 sites ranges from 4.10 to 90.71 mgl^{-1} (Table 4.3), with an overall mean of 19.95 (±17.10) μgl^{-1} (Table 4.2). The frequency histogram illustrated in Figure 4.3d show a similar positive skew as Chla, with the majority of sites (52%) having mean annual concentrations in the range 0-15.0 μgl^{-1}. According to OECD (1982) criteria, Figure 4.4c indicates a similar categorization of sites to that seen for Chla, although slightly more sites are classified as oligotrophic.

Secchi depth (SD) and Minimum Secchi depth (SD_{min})

Annual mean SD for the 46 sites ranges from 0.56 to 6.17 m (Table 4.3) with an overall dataset mean of 2.54 (±1.26) m (Table 4.2). Figure 4.3g indicates that the data have a slightly positively skewed distribution. 70% of sites have an annual mean SD <3.0 m (22%: <1.5 m, 48%: 1.5-3.0 m). According to the OECD (1982) criteria, most (48%) of the reservoirs in this dataset can be classified as 'eutrophic', with SD between 1.5 and 3.0 m. 28% of sites fall into the 'mesotrophic' category, with 22% classified as 'hypereutrophic' (Figure 4.4d). Only one site (37) is 'oligotrophic', with a secchi depth over 6.0 m. Figures 4.3h and 4.4e show that the frequency distribution of SD_{min} follows a similar trend to that displayed by SD, although less sites are classified as hypertrophic. Possible reasons for this could be similar to those described in the previous section in relation to Chla.

Figures 4.5d illustrates that SD exhibits some degree of seasonality, although numbers of measurements used in the box-plots for each season are inconsistent. The lowest transparencies and range in measurements occur in the winter (January 2000 median: 1.40 m). Transparencies are at their highest in the early summer (May 1999 median: 3.10 m, June 2000 median: 2.70 m) but SD decreases towards the late summer and autumn

(September 2000 median: 2.00 m). The low transparencies seen in the late summer / autumn are probably due to high levels of algal productivity, whereas the low winter transparencies are most likely a reflection of autochthonous wind-induced sediment resuspension and inflow of suspended particles from allochthonous catchment sources. It is therefore suggested that SD reflects both phytoplankton and inorganic and detrital turbidity and may also reflect dissolved coloured substances in the water (Moss *et al.*, 2003). It is noted that in the current study few sites show evidence of humic substances in their waters, therefore it is thought that SD largely reflects the two former potential sources of turbidity. Canfield & Bauchman (1989) note that non-algal particulate materials may be more important in influencing SD in artificial than in natural waterbodies.

Dissolved silica (SiO_2-Si)

Annual mean SiO_2-Si concentrations for the 46 sites range from 0.4 to 8.1 mgl^{-1} (Table 4.3), with an overall dataset mean of 3.45 (±2.43) mgl^{-1} (Table 4.2). These values are comparable to those observed in many other temperate, eutrophic lakes (e.g. Bennion & Smith, 2000; Gibson, 1986, 1988; Willén, 1991). Figure 4.3q shows that the data follow an approximately normal distribution. Most sites (76%) have values in the range 1.5-4.4 mgl^{-1}, with only one site (29) having an annual average concentration <0.5 mgl^{-1}. This indicates that in all but one reservoir there is on average sufficient Si (>0.5 mgl^{-1} (Pearsall, 1932)) dissolved in the water to enable freshwater diatom production.

Figure 4.5h illustrates the very clear seasonal pattern displayed by SiO_2-Si. Concentrations are highest in the winter (January 2000 median: 5.15 mgl^{-1}), then begin to fall rapidly throughout the spring (March 2000 median: 4.08 mgl^{-1}), reaching their lowest values in early summer (May 1999 median: 1.50 mgl^{-1}, June 2000 median: 1.94 mgl^{-1}), before increasing in the late summer / autumn period (September 2000 median: 2.52 mgl^{-1}, October 1999 median: 2.89 mgl^{-1}). This trend conforms to the general pattern observed in temperate lakes, and can be explained by the close correlation between diatom growth phases and the availability of dissolved Si (Bailey-Watts *et al.*, 1976a,b).

Figure 4.5i shows that the Si:TP ratio is seasonally variable. The trend is similar, but less pronounced than that seen for SiO_2-Si (Figure 4.5h), with the highest ratios in the winter and lowest ratios as the growing season progresses. Table 4.5 illustrates the large seasonal variations in Si:TP ratios for four selected sites. Since phytoplankton distribute themselves along resource ratio gradients using relative competitive abilities (Kilham, 1986), shifts in these ratios may be important in determining the seasonal succession of different species

both within and between algal groups. For example, declining Si:TP ratios favour the replacement of araphid diatoms by small centric diatoms as demand for SiO_2-Si increases (Tilman *et al.*, 1982). These ideas will be explored further in ensuing chapters.

Season	Year	Site number and name			
		2 Blackbrook	24 Porth	31 Swithland	36 Upper Tamar
May	1999	34	13	25	0
July	1999	4	113	68	37
October	1999	21	132	50	45
January	2000	57	149	110	47
March	2000	57	81	18	14
June	2000	17	64	75	4
September	2000	16	166	16	31
Mean		29	103	52	25

Table 4.5 Seasonality of the Si:TP ratio in selected reservoirs.

pH (pH) and Alkalinity (Alk)

Annual mean pH values for the 46 sites range from 6.65 to 8.59 (Table 4.3), with an overall dataset mean of 7.93 (±0.57) (Table 4.2). Figure 4.3i reveals a strongly negative skew, indicating that the majority of sites are alkaline, having pH values above the mean. Only two sites (34 and 29) have values <7.00 and most sites (54%) have annual average pH values in the range 8 to 8.5. Figure 4.5j illustrates that pH has relatively low intra-annual variation. pH is lowest in the winter (January 2000 median: pH 7.70) and highest during the growth season (March 2000 median: pH 8.24 – September 2000 median: pH 8.15) however the differences are minimal.

Alk concentrations display a normal distribution across the annual mean range 7 to 207 mgl^{-1} (Table 4.3), with an overall dataset mean of 91 (±53) mgl^{-1}, indicating that the majority of reservoirs are well buffered against changes in pH. Figure 4.5k illustrates that Alk behaves conservatively, with concentrations exhibiting very little inter-annual variation and showing no clear seasonal trend. Alk is the most stable water chemistry variable measured in the calibration dataset.

The sites displaying the lowest pH values (<7.00) and Alk (<12 mgl^{-1}) have catchments that are located on base-poor granite bedrock with heathland or coniferous catchments (sites 29 and 34). Sites with pH values in the range 7.00 to 8.00 and Alk concentrations between 20 and 110 mgl^{-1}, have catchments that are largely comprised of base-poor bedrocks, such as sandstones, siltstones, slates and grits. Such bedrocks include the Lower Cretaceous Hastings Beds (sites 39, 41, 43, 44, 45) in the southeast, the Upper Devonian Ilfracombe

Slate series (sites 8, 37, 38), Lower Devonian Meadfoot Beds (site 24) and Westphalian Bude formation (site 36) in the southwest, Triassic Arden Sandstone (sites 2, 10, 31) in the Midlands, and Carboniferous Millstone Grit (sites 22 and 33) in the north of the study area. The majority of sites in the current study have pH values in the range 8.00 to 8.60 and Alk concentrations in the range 90 to 190 mgl^{-1}, with catchments that are situated on base-rich bedrock geology. This consists predominantly of clays, including Jurassic Lias Clays (sites 11, 13, 23, 25, 26, 27, 46) and Oxford Clays (sites 15, 16), and mudstones e.g. Triassic Keuper Marls (sites 3, 4, 7, 12).

Conductivity (EC), Na^+, K^+, Ca^{2+}, Mg^{2+}, Cl^-, Geology (Geol) and Altitude (Alt)

Annual average conductivities across the 46 sites range from 110 to 887 μScm^{-1} (Table 4.3), with an overall dataset mean of 419 (±186) μScm^{-1} (Table 4.2). 39% of the reservoirs have values in the range 400 to 599 μScm^{-1} with no sites possessing conductivities >1000 μScm^{-1} that could be termed 'brackish', although site 16 is an outlier with an annual mean of 887 μScm^{-1}.

Table 4.2 shows that the order of abundance of the major cations in this dataset (in mgl^{-1}) is: Na^+ (13.98 ±7.96) >Ca^{2+} (13.7 ±9.79) >Mg^{2+} (4.23 ±3.43) >K^+(3.90 ±1.83). The order of abundance of the major anions cannot be assessed since only Cl^- was measured, but Cl^- has a concentration more than double that (33.41 ±17.32) of any measured cation in the dataset, indicating its likely importance in the lowland reservoirs. The high concentrations of Na^+ and Cl^- could be explained by road salt inwash, used as a de-icing agent to improve winter driving conditions (Sutcliffe & Carrick, 1983a,b; Beebee, 1987; Gibson, 1989), or instead by the inflow of sewage effluent (Sutcliffe & Carrick, 1983a,b; Harper & Stewart, 1987). Cl^-, Na^+, Ca^{2+} and Mg^{2+} show frequency distributions that are positively skewed, whereas K^+ follows a normal distribution (Figures 4.3l-p). The concentrations of the cations and Cl^- are positively correlated with EC. The generally high cation concentrations across the dataset may be associated with the large number of sites with catchments on base-rich geology (52%: Figure 4.3r). The geographical distribution of conductivity values broadly follows the pattern of pH and Alk.

Altitude ranges from 0 – 240 m.a.O.D., with a mean value of 93.87 (±62.04) (Table 4.2). Figure 4.3z shows that the majority of sites are low-lying, with 83% at altitudes of <150 m.a.O.D. and only 11% of sites located above 200 m.a.O.D. This perhaps indicates that the overall high concentrations of cations present in the reservoir waters are largely catchment-derived, since weathering rates and erosion increase at lower altitudes (Rioual, 2002).

Similar relationships between chemistry and altitude have been observed in Great Britain (Kernan, 1998) and Switzerland (Müller *et al.*, 1998).

Mean and Maximum Depth (Z_{mean} & Z_{max}), Reservoir capacity (Vol), Reservoir surface area, & presence/absence of destratification equipment (Destrat).

Reservoir capacity (Vol) ranges from 120-124000 Ml with an overall mean of 9646 ±20190). Figure 4.3u shows a positive skew, with 39% of reservoirs having capacities of 500-2500 Ml. Reservoir surface area follows a similar positive skew (Figure 4.3v). The mean value for Z_{max} is 15.2 m, with a range of 5.0-35.0 m. The majority (43%) of reservoirs have maximum depths in the range 10-14.9 m (Figure 4.3s), which is sufficient for the development of thermal stratification. Overall, 61% of the 46 reservoirs use destratification equipment (Figure 4.3x) to alleviate the problems of algal blooms associated with a stable water column during the period of thermal stratification. However this percentage increases as the maximum depth of the reservoir increases: 70% of reservoirs with Z_{max} >10 m and 82% with Z_{max} >15 m are equipped with destratification equipment, indicating that stratification seldom occurs in any reservoir.

Reservoir water source (Type), Catchment size (Cat) and % Agricultural land use (Agri).

Figure 4.3w illustrates that 48% of sites are impounding reservoirs, 22% receive water from both their natural catchment and pumped sources, 26% are pumped storage facilities and 4% are spring-fed. Impounding reservoirs have the largest natural catchments, because their only water source is catchment-derived. Overall however, natural catchment sizes are generally small, with 76% <24 km^2 (Figure 4.3aa). Catchment land use, of those reservoirs with natural catchments, is dominated by agriculture, with 67% having >60% agricultural land use (Figure 4.3ab).

4.4 Relationships between environmental variables

The previous section explored the trends exhibited by individual environmental variables in the dataset and variations in the ratios between some of these variables. This section considers the relationships between variables by graphically and statistically displaying their regressions and correlations. Most attention will be focussed on the relationships between nutrients and environmental variables of particular importance in determining algal productivity and composition, with specific reference to reservoir trophic status.

4.4.1 Overview of relationships between environmental variables

To provide an initial indication of relationships between variables, a multiple scatter-plot was constructed for the full dataset of 46 sites and 26 environmental variables (Figure 4.6). Table 4.6 displays a product-moment correlation matrix showing Pearson's correlation coefficients for each pair of environmental variables displayed in Figure 4.6, enabling the statistical significance and strength of correlations between variables to be assessed. In the following section the correlation coefficients between variables are displayed in parentheses (perfect positive correlation = 1, perfect negative correlation = -1).

A large number of the set of 26 measured environmental variables are correlated either at the 95% ($P<0.05$: significant) or 99% ($P<0.01$: highly significant) confidence level (Table 4.6). It is noted that although many correlations are highly significant, the percentage of variance explained is generally rather low.

Highly significant positive correlations exist between the pairs of variables: TON and TN (0.91), and SRP and TP (0.82). These results indicate that the total nutrient concentrations of TN and TP increase in line with their corresponding biologically available counterparts TON and SRP.

Results show that Chla and ChlaM are highly correlated (0.71), indicating that, in general, reservoirs with high mean annual Chla also have high annual maxima. SD and Z_{mean} and Z_{max} (0.40 and 0.45 respectively) are positively correlated, indicating that mean annual water transparency is related to reservoir water depth. Significant negative correlations are found between Chla and SD (-0.54), ChlaM and SD (-0.55), Chla and Z_{mean} and Z_{max} (-0.57 and –0.51 respectively), ChlaM and Z_{mean} and Z_{max} (-0.61 and –0.58 respectively), ChlaM and Vol (-0.40). A highly significant positive correlation is found between, reservoir Age and ChlaM (0.44). Age and Z_{mean}, Z_{max} and Vol (-0.51, –0.53 and –0.52 respectively) are negatively correlated. These correlations indicate that water transparency is related to algal productivity, and that in turn, water transparency is largely determined by reservoir water depth and volume, which in turn reflects reservoir age. Thus, the shallowest reservoirs are generally the oldest, most productive and turbid sites. This pattern may occur because many of the older reservoirs have a greater accumulation of sediments and thus a larger internal store of nutrients, which can in turn support high algal production. Many older reservoirs are also of the impounding type, set in shallow natural catchments. Their morphology is a function of the original reservoir design, which may also be a function of the era in which

Alk	0.76																								
EC	0.69	0.85																							
TON			0.33																						
TN		0.43	0.45	0.91																					
SRP	0.39	0.59	0.55	0.34	0.41																				
TP	0.40	0.58	0.64		0.30	0.82																			
Chl	0.37																								
ChlM	0.42	0.40					0.39	0.71																	
SD							-0.40	-0.54	-0.55																
Si		0.35	0.34			0.38	0.41																		
Na	0.34	0.39	0.78			0.37	0.60																		
K	0.41	0.46	0.75		0.29	0.52	0.69					0.84													
Cl	0.33	0.38	0.77			0.30	0.50					0.95	0.75												
Ca	0.44	0.65	0.76			0.45	0.55					0.55	0.58	0.52											
Mg	0.56	0.44	0.50			0.41	0.35		0.31			0.40	0.35	0.44											
Z_{max}								-0.51	-0.58	0.45															
Z_{mean}								-0.57	-0.61	0.40							0.88								
Age				-0.33				0.35	0.44		0.37						-0.53	-0.51							
Type			0.42	0.31		0.53	0.58					0.57	0.49	0.47	0.45		0.31	0.38	-0.45						
Geol	0.74	0.71	0.71		0.35	0.35	0.40					0.40	0.50	0.37	0.56		-0.30	-0.32							
Destr																	0.44	0.33	-0.32						
Alt	-0.38	-0.45	-0.46	-0.32		-0.33	-0.50		-0.44	0.46		-0.42	-0.34	-0.34	-0.30		0.35			-0.40	-0.34				
Vol						0.33		-0.32	-0.40	0.34	-0.31		0.52		0.32		0.66	0.53	-0.52	0.35		0.55			
Cat													0.32											0.54	
%Agri											-0.32												0.50		0.71
	pH	Alk	EC	TON	TN	SRP	TP	Chl	ChlM	SD	Si	Na	K	Cl	Ca	Mg	Z_{max}	Z_{mean}	Age	Type	Geol	Destrat	Alt	Vol	Cat

Table 4.6: Product-moment correlation matrix between all environmental variables measured for the 46 sites. Only significant (P<0.05) correlations are shown. Highly significant (P<0.01) correlations are shaded.

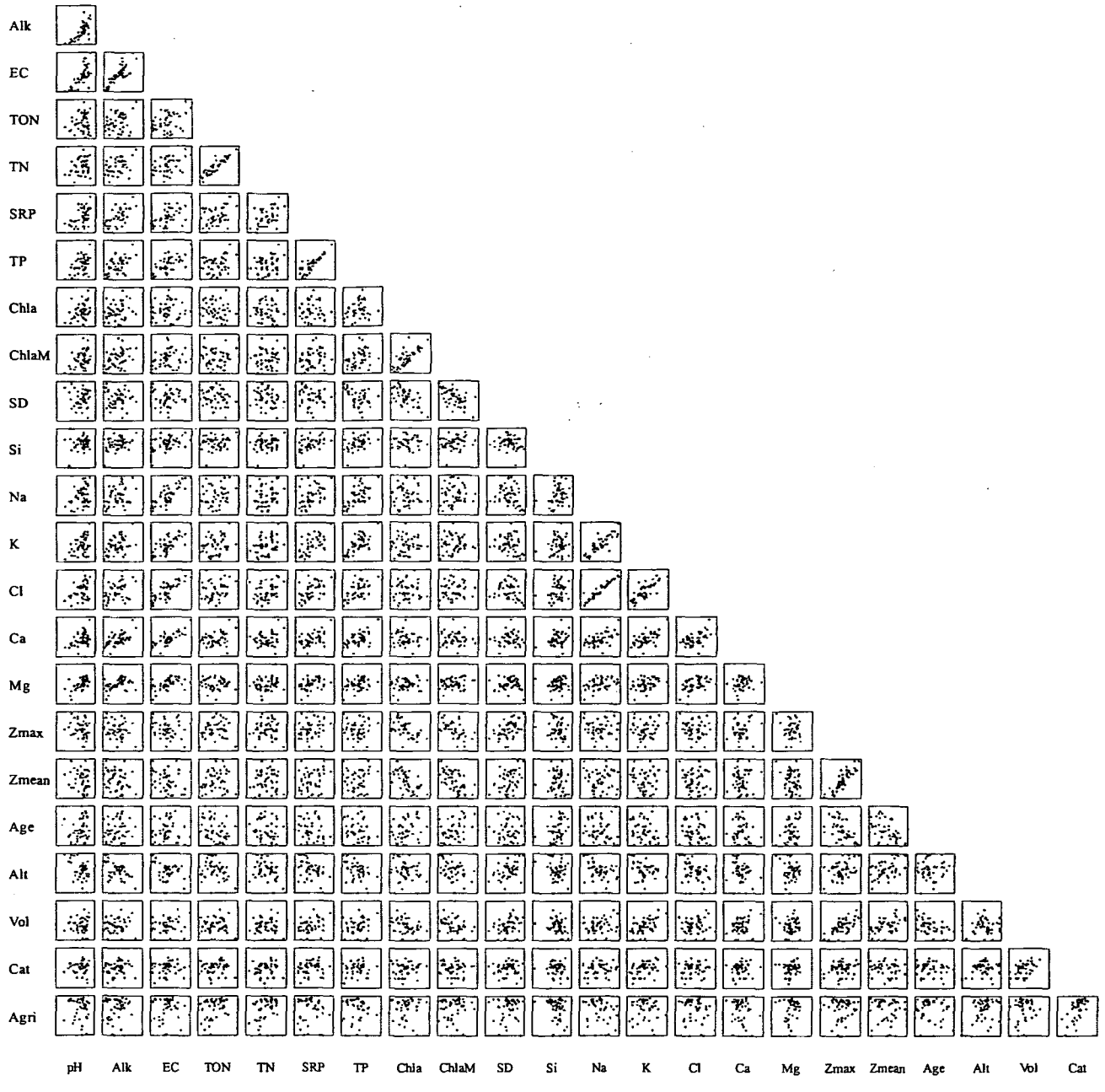


Figure 4.6: Multiple scatter-plots graphically displaying the relationships between 23 environmental variables (nominal variables have been omitted)

the reservoirs were constructed. In addition, construction of many older impounding reservoirs may have unwittingly occurred within eutrophic river catchments. Reservoirs constructed in the second half of the 20th century are generally of the pump-storage type, with small natural catchments but sources supplemented with water pumped in from large rivers located in different catchments.

The relationships between different nutrients are not as highly correlated as might be expected e.g. SRP and TN (0.41), SRP and TON (0.34), TN and TP (0.30). TON and TP were non-significantly correlated. The only significant correlations between nutrients and algal productivity are seen between TP and ChlaM (0.39). There is a highly significant positive correlation between TP and Si (0.41) and SRP and Si (0.38). This contrasts with the general pattern seen in moderately deep, temperate lakes in which an increase in P corresponds to Si reduction (Schelske, 1988). Instead, the trend seen in this study is more commonly reported for shallow lakes (Bennion & Smith, 2000), perhaps reflecting the polymictic nature of many of the deeper reservoirs that is achieved through summer destratification. Artificial destratification mixes the water column, heating the hypolimnetic waters of deeper reservoirs, which would retain cool hypolimnia under naturally stratified conditions. Silica solubility is known to increase at higher pH values and higher temperatures (Bailey-Watts, 1989 a & b; Willén, 1991) and release of P from sediments has been shown to increase at elevated pH levels in summer in response to elevated photosynthetic activity (Søndergaard *et al.*, 1988). A possible explanation for the simultaneous increase in both P and Si, is that both P and Si are largely derived from the sediments (Bennion & Smith, 2000). In common with Bennion (1995), although diatom preservation in the surface sediments was generally good, fossil material lying beneath the most recently accumulated 'death' assemblage, regularly showed evidence of dissolution.

There are highly significant positive correlations between TP and K (0.69), TP and EC (0.64), TP and alkalinity (0.58), TP and pH (0.40). Other highly significant positive correlations are found between Na^+ and Cl^- (0.95), Na^+ and K^+ (0.84), K^+ and Cl^- (0.75), EC and alkalinity (0.85), pH and Alk (0.76), EC and Na^+, K^+, Ca^{2+}, Cl^- and Mg^{2+} (0.78, 0.75, 0.76, 0.77 and 0.50 respectively), Geol and pH, Alk, EC, Na^+, K^+, and Ca^{2+} (0.74, 0.71, 0.71, 0.40, 0.50 and 0.56 respectively) and pH and EC (0.69). These results are unsurprising since the ionic status and pH of a reservoir's water would be expected to depend upon and hence reflect the geological composition of the catchment. EC and its constituent ions and pH, alkalinity and catchment geology are essentially explaining much the same variation in the environmental dataset.

The significant correlations described and discussed above indicate that there is a large amount of multi-colinearity within the environmental variable dataset. Variables that are highly inter-correlated are essentially describing similar axes of variation within the dataset. Information gleaned from the correlation data in this section will enable objective sequential removal of inter-correlated variables in the subsequent direct gradient ordination chapter. The aim of this process will be to reduce the environmental dataset to the minimum number of explanatory variables that still describe a large amount of the variance within the species dataset.

4.4.2 Regressions between environmental variables

Nutrients, algal productivity and water clarity

In linear regressions the relationship between $\log_{10}$ mean TP and $\log_{10}$ mean Chla can only be described as very weak (R^2 = 0.016) and the variables non-significantly (P = 0.40) correlated (Figure 4.7a). This is surprising because most authors reveal clearly discernable linear relationships or (more commonly) sigmoidal fitted curves between these parameters. The strength of the relationship between the variables is improved in the current study (R^2 = 0.16) and shows a highly statistically significant (P = 0.007) positive correlation when $\log_{10}$ mean TP and $\log_{10}$ ChlaM are regressed (Figure 4.7c). However, the relationship is still less strong than those described in the literature (e.g. Sakamoto, 1966; Dillon & Rigler, 1974; Smith, 1982; Canfield, 1983; McCauley *et al.*, 1989; Prairie *et al.*, 1989).

Canfield & Bachmann (1981) compared the relationship between $\log_{10}$ TP and $\log_{10}$ Chla in natural and artificial lakes and found the correlation between these variables to be weaker in artificial systems (i.e. reservoirs). They ascribed the weaker relationship in artificial lakes to the increased influence of allochthonous inorganic particulate material and elevated phosphorus sedimentation rates. These observations would go some way towards explaining the weak correlation seen in the current dataset and may indicate that factors other than nutrients (e.g. temperature, light, wind strength, inflow sources and residence time of the reservoir water) are limiting algal populations, possibly through the presence of non-algal turbidities. If this were the case, then it might be expected that the relationship between Chla and SD in artificial reservoirs would also be weaker than in natural systems. Indeed, this appears to hold true based on results from the current study. The relationship between Chla and SD (Figure 4.7e) shows a statistically significant negative relationship (R^2 = 0.32, P = <0.01) and ChlaM and SD_{min} (Figure 4.7f) show a slightly stronger relationship (R^2 = 0.56, P = <0.01). However, Canfield & Bachmann (1981) reported stronger relationships

between Chla and SD in natural lakes (R^2 = 0.83) and weaker relationships in artificial lakes (R^2 = 0.44). The latter figure compares favourably with those obtained from the reservoirs in this study, further supporting the suggestion that non-algal turbidities are important determinants of water clarity in many artificial lakes. These non-algal turbidities could originate from sediment-laden inflow sources, destratification equipment causing disturbance of reservoir sediments or perhaps the re-working of exposed littoral sediments during periods of drawdown.

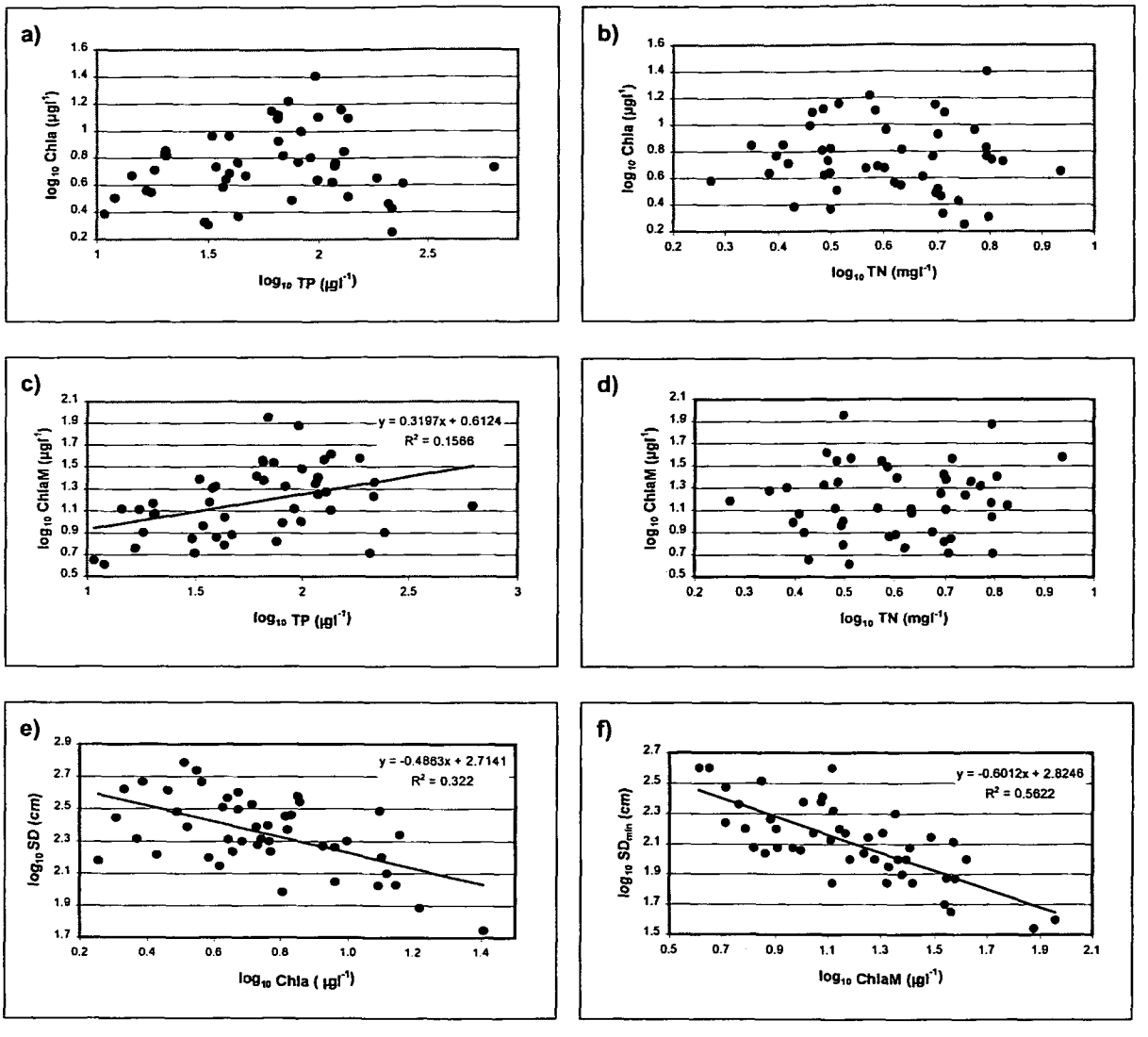


Figure 4.7 **Scattergrams illustrating relationships in the 46-reservoir dataset between a) mean log_{10} Chla and log_{10} TP concentrations (P = 0.38: non-significant); b) mean log_{10} Chla and log_{10} TN concentrations (P = 0.68: non-significant) c) log_{10} ChlaM and mean log_{10} TP concentrations (P = <0.01: highly significant); d) log_{10} ChlaM and mean log_{10} TN concentrations (P = 0.54: non-significant);e) mean log_{10} Chla and log_{10} SD (P = <0.01: highly significant); f) log_{10} ChlaM and log_{10} SD_{min} (P = <0.01: highly significant).**

Prairie *et al.* (1989) and McCauley *et al.* (1989) demonstrated that the relationship between $\log_{10}$ Chla and $\log_{10}$ nutrients (TP and TN) is best described by a sigmoidal curve rather than by a straight line (Smith, 1982). However, the dataset in this study constitutes a far smaller number of lakes and covers only short sections of the long Chla, TP and TN gradients utilised by Prairie *et al.* (1989). For $\log_{10}$ TP vs. $\log_{10}$ Chla, the current dataset spans only the central portion of the sigmoidal curve (Figure 4.8). Thus it fails to capture the low Chla values and fails to reach the 'plateau' or 'asymptote' of the sigmoidal curve i.e. the maximum Chla concentration above which any further increase in TP does not result in higher Chla concentrations, a phenomenon termed 'self-shading' by Reynolds (1984).

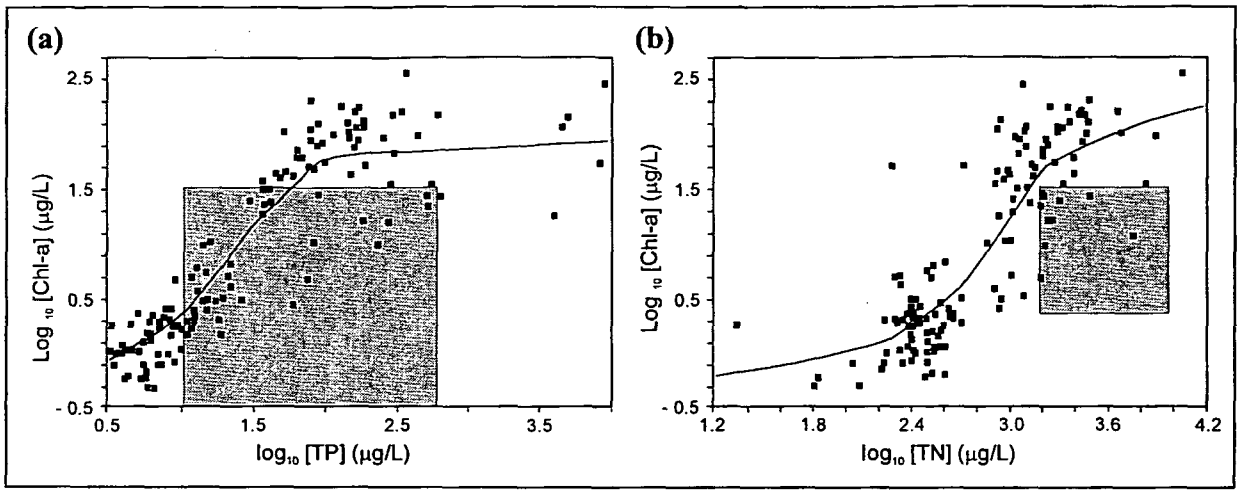


Figure 4.8 Relationships between (a) Chla and TP; (b) Chla and TN. Data are taken from Prairie *et al.* (1989). Shaded boxes indicate the range of values covered by the 46 reservoirs sampled in the current study.

For $\log_{10}$ TN vs. $\log_{10}$ Chla, data in the current study consist of high TN values relative to the range utilised by Prairie *et al.* (1989). Consequently they fall to the right of the published sigmoidal curve, and no significant relationship is exhibited between $\log_{10}$ TN and $\log_{10}$ Chla. ($P = 0.68$) (Figure 4.7b). A non-significant relationship is again obtained when $\log_{10}$ TN and $\log_{10}$ ChlaM are regressed ($P = 0.54$) (Figure 4.7d). The weak relationships between TN and Chla(M) provides evidence that overall, the reservoirs in this dataset are not nitrogen limited. However, since the supply ratios of different nutrients are often important in determining algal productivity and the relative competitive abilities of different algal species, this observation may be an over-simplification.

TP and TN

Figure 4.9a illustrates the relationship between $\log_{10}$ TP and $\log_{10}$ TN. Although the relationship is significant at the 95% level ($P = 0.04$), it is weak ($R^2 = 0.09$), with a Pearson's correlation coefficient of 0.30. This shows that whilst there is a relationship

between TP and TN, it is perhaps more informative to examine the relative supply ratios as opposed to viewing these nutrients as separate entities (section 4.3.2). Such ratios can show which of the nutrients is limiting, both generally and on a seasonal basis.

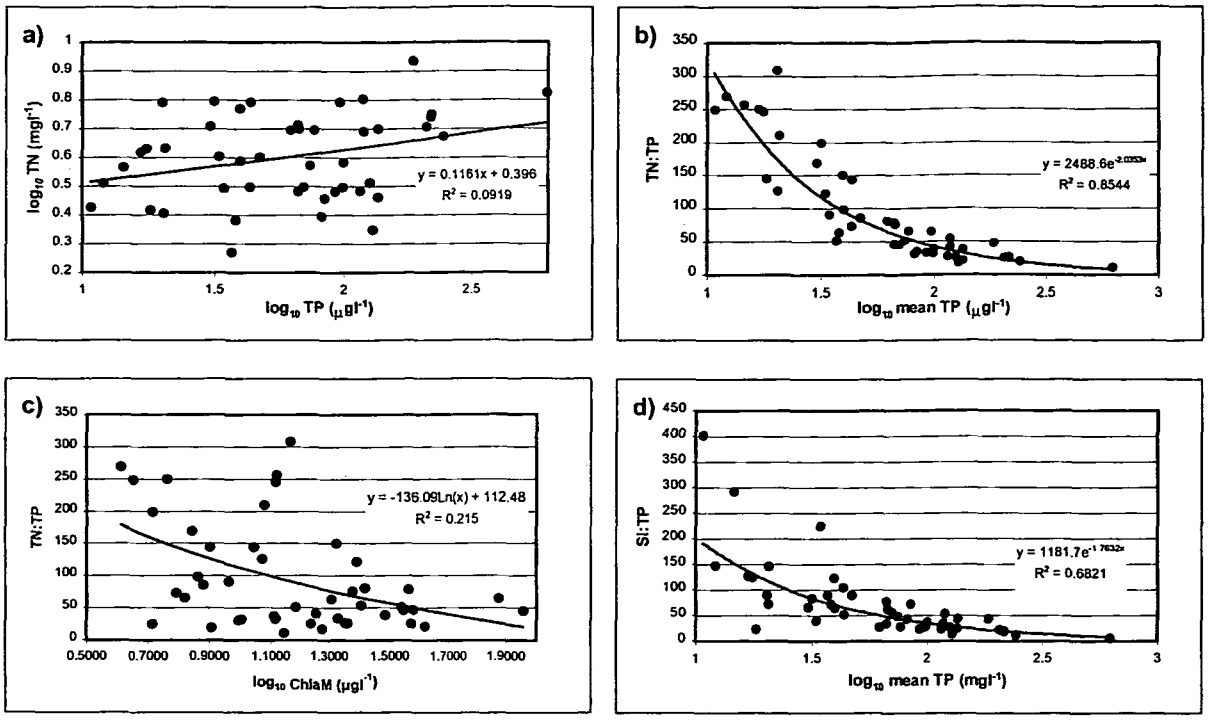


Figure 4.9 **Scattergrams illustrating relationships in the 46-reservoir dataset between a) mean log_{10} TP and log_{10} TN concentrations (linear trend line fitted) (P = 0.041: significant); b) the ratio of TN:TP and mean log_{10} TP concentration (exponential trend line fitted) (P = <0.01: highly significant); c) the ratio of TN:TP and log_{10} ChlaM concentration (power trend line fitted) (P = <0.01: highly significant); d) the ratio of Si:TP and mean log_{10} TP concentration (exponential trend line fitted) (P = <0.01: highly significant).**

Nutrient ratios as a function of TP and ChlaM

When the ratio of total nitrogen to total phosphorus (TN:TP) is plotted as a function of log_{10} TP (Figure 4.9b), the data follow a strong 'exponential' relationship ($R^2 = 0.85$, P = <0.01). This is a similar to the trend presented by Seip *et al.* (2000) for a suite of Nordic lakes, however these authors do not present regression statistics to allow statistical comparison. Results from the current study place sites with the lowest TP concentrations and also the highest TN:TP ratios (e.g. sites 29 and 37) to the left of the regression plot, and sites with high TP concentrations, but low TN:TP ratios (e.g. 6 and 16) towards the right (Figure 4.9b). As discussed in section 4.3.2, the TN:TP ratio can be important in determining phytoplankton community structure. Low epilimnetic N:P ratios are reported to favour the dominance of bloom-forming cyanophytes (e.g. Schindler, 1977; Tilman & Kiesling, 1984). However, cyanophytes are generally considered to be poor competitors for P (e.g. Stockner

& Shortreed, 1988). Such eutrophic reservoirs with high TP concentrations and low TN:TP ratios (i.e. sites located towards the left of Figure 4.9b) are likely to favour cyanophytes.

Figure 4.9c illustrates that there is a power relationship between TN:TP and $\log_{10}$ ChlaM. Although the relationship is only weakly significant it does indicate that TN becomes limiting in proportion to the availability of TP as algal productivity increases. The seasonality of the TN:TP ratio is illustrated in Figure 4.5g, showing that the TN:TP ratio decreases throughout the summer. This supports the observation that algal productivity in the late summer period is largely composed of those species favouring low TN:TP ratios e.g. cyanophytes.

Si:TP ratios as a function of TP

In section 4.3.2, reference was made to seasonality of the Si:TP ratio in selected reservoirs (Table 4.4). Figure 4.9d shows that the Si:TP ratio varies as a power function of $\log_{10}$TP, with the highest Si:TP ratios found at the lowest TP concentrations. This indicates that in those sites with high levels of TP, Si could be limiting. During periods of high demand for Si (e.g. diatom bloom seasons), this could lead to Si depletion in the water column and in turn, if the water column is well-mixed, Si could be recycled from the sediments and hence enhance diatom dissolution at the sediment-water interface (Bailey-Watts, 1976a,b). However, Conley *et al.* (1988) reported that, in Lake Michigan, only a small proportion of the Si needed to support the annual diatom production was internally regenerated by the flux of Si across the sediment-water interface. Under steady-state conditions, a combination of the increased demand for Si, its slow rate of recycling, and the low rates of internal regeneration would result in Si depletion in eutrophic lakes (Stoermer *et al.* 1985, Schelske *et al.* 1986). Ultimately, low Si:TP ratios may result in the displacement of Si-limited diatoms by non Si-requiring species (Reynolds, 1984, Tilman *et al.* 1986). These ideas will be explored further in subsequent chapters.

4.5 Ordination and classification of sites using the environmental data

Principal Components Analysis (PCA) is the main ordination method utilised in this section to detect the major gradients in the dataset and to identify outliers with extreme or unusual environmental characteristics. Classification techniques are then used to group sites according to their environmental attributes so that a visual display of the similarity / dissimilarity of sites arranged according to axes of variation within the environmental data can be seen. Ordination and classification of sites according to the measured environmental

variables carried out in this section provides data and valuable information for input into subsequent direct gradient analyses (Chapter 5) and inference model creation (Chapter 7).

4.5.1 Data Transformations

The mean annual data for all 26 environmental variables were tested statistically for normality in MINITAB™ Release 13.31 (Minitab Inc™, 2000) using the Anderson-Darling normality test. This tests the null hypothesis that the data follow a normal distribution. If the p-value of the test is *less* than a rejection level of 0.05 (95% confidence level), then the null hypothesis is rejected, and the data *do not* follow a normal distribution. Type, Geol and Destrat were not transformed since they are measured on a nominal scale. Table 4.7 displays the results. K^+, alkalinity and EC displayed strong normal distributions and hence did not require transformation. Most other variables required $\log_{10}$ transformation to reduce the skew in their distributions. According to the Anderson-Darling normality test, all but four (pH, Alt, Agri and Ca^{2+}) of the environmental variables that initially failed to meet the assumption of normality fulfilled this assumption following $\log_{10}$ transformation. Alt, Agri and Ca^{2+} achieved normality following a square root transformation. pH did not achieve normality despite various attempts at transformation, thus untransformed $\log_{10}$ scale values were used.

Variable	Before transformation: (P value)	Normally distributed?	After **$\log_{10}$** transformation: (P value)	Normally distributed?	After **Sq root** transformation: (P value)	Normally distributed?
Alk	0.615	Yes	N/A	N/A	N/A	N/A
K	0.573	Yes	N/A	N/A	N/A	N/A
EC	0.250	Yes	N/A	N/A	N/A	N/A
ChlaM	0.055	Yes (weak)	0.844	Yes	N/A	N/A
TN	0.053	Yes (weak)	0.213	Yes	N/A	N/A
SD	0.040	No	0.890	Yes	N/A	N/A
Z_{max}	0.005	No	0.863	Yes	N/A	N/A
Vol	0.000	No	0.853	Yes	N/A	N/A
Chla	0.000	No	0.675	Yes	N/A	N/A
TP	0.000	No	0.608	Yes	N/A	N/A
Mg	0.000	No	0.572	Yes	N/A	N/A
Na	0.000	No	0.566	Yes	N/A	N/A
TON	0.042	No	0.522	Yes	N/A	N/A
Z_{mean}	0.034	No	0.375	Yes	N/A	N/A
Cl	0.000	No	0.291	Yes	N/A	N/A
Si	0.055	No	0.224	Yes	N/A	N/A
SRP	0.000	No	0.188	Yes	N/A	N/A
Age	0.000	No	0.104	Yes	N/A	N/A
Cat	0.000	No	0.098	Yes	N/A	N/A
Alt	0.015	No	0.014	No	0.566	Yes
Ca	0.000	No	0.029	No	0.385	Yes
Agri	0.000	No	0.000	No	0.114	Yes
pH	0.006	No	0.002	No	0.003	No
Type	N/A	N/A	N/A	N/A	N/A	N/A
Geol	N/A	N/A	N/A	N/A	N/A	N/A
Destrat	N/A	N/A	N/A	N/A	N/A	N/A

Table 4.7: Data transformations required for the 26 environmental variables (shaded boxes indicate transformations required to achieve normal distributions for each variable)

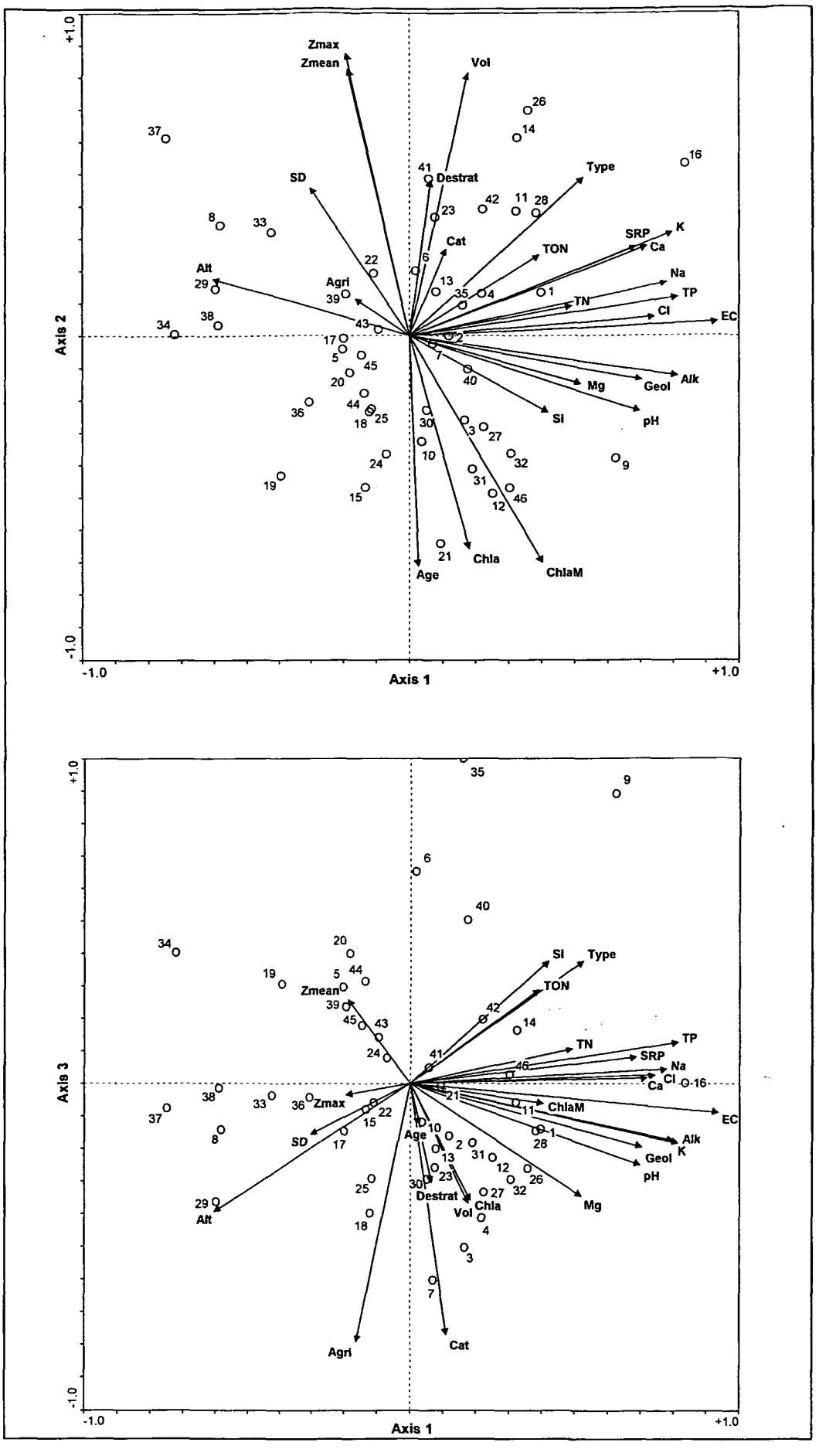
4.5.2 Ordination (PCA) of the full dataset

A standard PCA analysis was performed in CANOCO for Windows 4 (ter Braak & Smilauer, 1998) to detect the major environmental gradients and identify outlier sites with extreme or unusual chemistry. PCA on a correlation matrix, with centring and standardisation of the environmental data was performed. Initially, all 46 sites and 26 environmental variables (data transformed as necessary – see Table 4.7) were treated as active samples. The eigenvalues and cumulative variance accounted for by the first four axes are listed in Table 4.8.

Axis	Eigenvalue	Cumulative % variance
1	0.301	30.1
2	0.186	48.8 (18.7)
3	0.097	58.5 (9.7)
4	0.071	65.6 (7.1)

Table 4.8: Results of PCA analysis on 46 sites and 26 environmental variables. (numbers in parentheses are individual axes contributions)

These values indicate that the 26 environmental variables account for a large proportion of the variance in the data. The percentage of the variance in the data explained by the first four axes is relatively high (65.6%). The difference in the relative sizes of axes 1, 2 and 3 is large (30.1%, 18.7% and 9.7% variance explained by axes 1, 2 and 3 respectively), suggesting that axis 1 represents the main gradient of variation in the environmental dataset, namely alkalinity, conductivity (and its associated ions), pH and phosphorus. This result was partially expected because the 46 sites were selected on the basis of maximising the TP gradient. However, at the time of site selection, it was not envisaged that the relationship between TP and pH / alkalinity / conductivity (and its associated ions) would be so pronounced, since this is in contrast to results presented by Bennion *et al.*, (1997) for shallow, lowland standing waters in the southeast region of England. These authors did not find a strong relationship between TP and bedrock geology. They suggested therefore that land-use in individual site catchments was largely controlling surface water phosphorus concentrations. In the current study however, catchment bedrock geology appears to have a significant effect on reservoir phosphorus concentrations, although the influence of catchment land-use cannot be discounted since land-use is to some extent determined by underlying geology. Percentage agricultural land-use (%Agri) was the only land-use factor entered into the PCA, with no distinction made between pastoral and arable agriculture and the relative importance of these agricultural land-uses in terms of nutrient supply to the reservoirs. Thus the non-significant relationship between %Agri and geology / nutrients



Figures 4.10a and 4.10b **PCAs illustrating axes 1 vs. 2 (4.10a) and axes 1 vs. 3 (4.10b) for 46 sites and 26 environmental variables.**

(Table 4.6) should not be over-interpreted, particularly since the correlation is further confounded by the influence of pump-storage reservoirs within the dataset, for which it is difficult to objectively determine catchment extent and land-use.

The PCA bi-plot of axis 1 against axis 2 derived from the 26 environmental variables and 46 active sites (Figure 4.10a) illustrates that the first axis is highly positively correlated with EC, Alk, pH, TP, SRP, Na^+, K, Cl and, to a lesser extent, Ca, Mg, Si, TON and TN. Therefore, axis 1 contrasts high nutrient, high pH and high conductivity sites on the right of the diagram e.g. sites 16 and 9, with low nutrient, low pH and low conductivity sites on the left e.g. 29 and 34. Small angles between the arrows in the bi-plot indicate high correlation between these variables. The product-moment correlation coefficient matrix (Table 4.6) confirms these observations for the variables associated with axis 1 (see section 4.4.1). Phosphorus and nitrogen concentrations are significantly, but only weakly correlated. A number of studies have shown that a poor relationship often occurs because as one plant nutrient increases, another becomes limiting (e.g. Gibson, 1986; Bennion et al., 1997).

Axis 2 is positively correlated with Chla, ChlaM and Age, and negatively correlated with $Z_{mean/max}$, SD and Vol, illustrating an inverse relationship between these two groups of variables. The results in Table 4.6 further indicate the statistically significant negative relationship between these two groups of variables associated with axis 2. Figure 4.7e adds support to the strong inverse relationship between Chla and SD. Figure 4.10b illustrates that Axis 3 is negatively correlated with catchment area and % agricultural land-use in the catchment.

4.5.3 Cluster analysis of the full dataset

The axis scores generated through PCA analysis of the full dataset (46 sites and 26 environmental variables) are less 'noisy' than the actual environmental data. This is because the number of variables is reduced and combined into components, which correspond to the main trends in the dataset. On this basis the PCA axis scores for the first two axes were substituted into the cluster analysis in place of the actual data for individual environmental variables to derive groups of similar sites (Everitt *et al.*, 2001). Groupings were for descriptive purposes only and were not carried forward in further analysis. Therefore the decision both to employ axis scores in place of raw data and to select the first two axes only, on which to perform the cluster analysis were subjective. The use of axis scores will always produce better clusters than use of raw data values, but if the clusters derived make intuitive environmental sense then this is justified. Selection of only the first two axis scores

facilitated better delineation and more environmentally intuitive description of site groupings. Cluster analysis was also performed on the first three axis scores to compare groupings. This produced similar groupings: Groups 1 and 2 were identical, however groups 3, 4 and 5 were less well delineated. This appears to be the result of the strong influence of %Agri and Cat on PCA axis 3. Thus axis scores for only the first two axes were used for cluster analysis. This was performed in PC-Ord 4 (McCune & Mefford, 1999) using Ward's method (Ward, 1963) of minimum variance clustering. The resultant cluster dendrogram and group membership is illustrated in Figure 4.11. The cut-off level of five groups was determined subjectively, although at the next level only one site was in the group. This site was determined an outlier and it subsequently considered for removal from the environmental dataset. The PCA ordination diagram with groupings applied is shown in Figure 4.12.

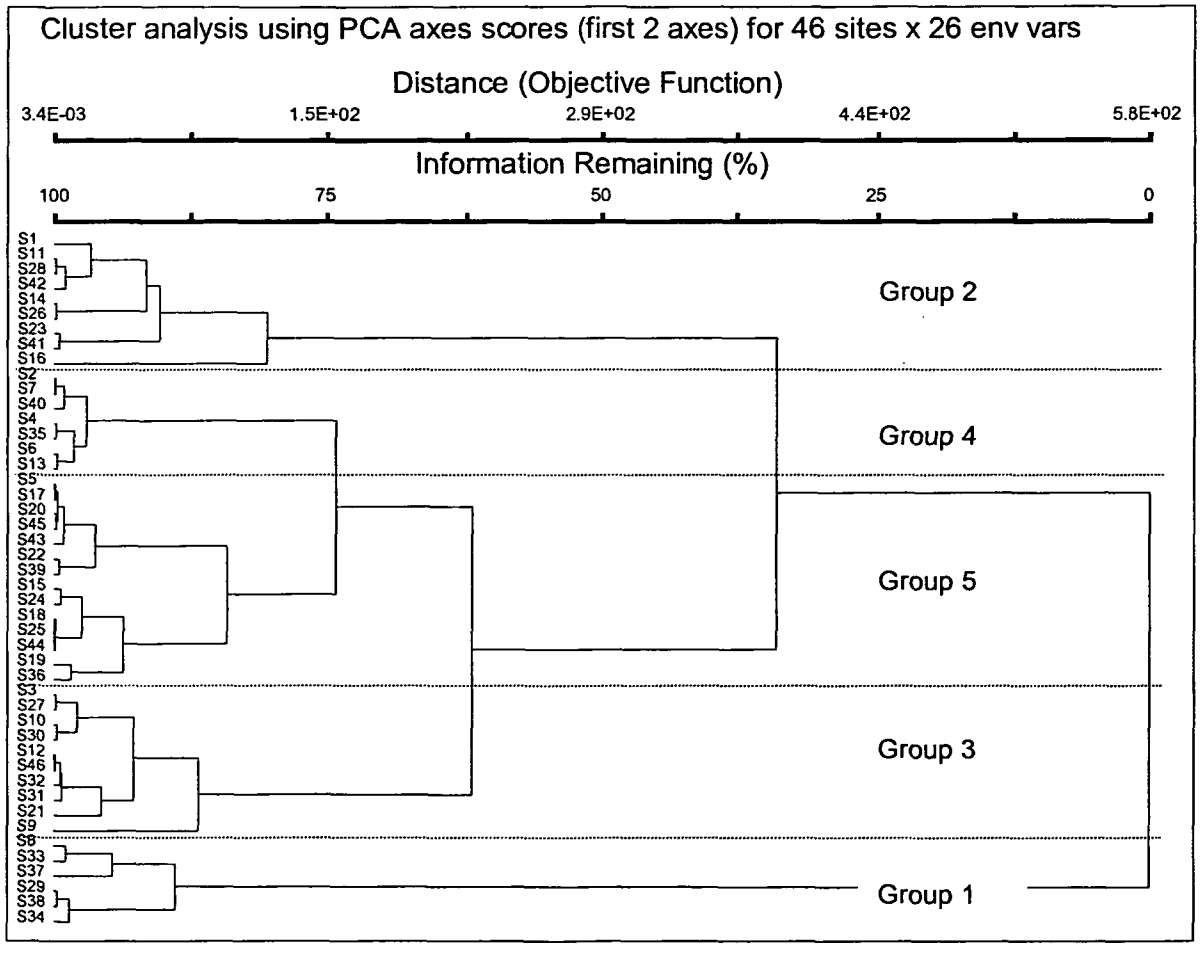
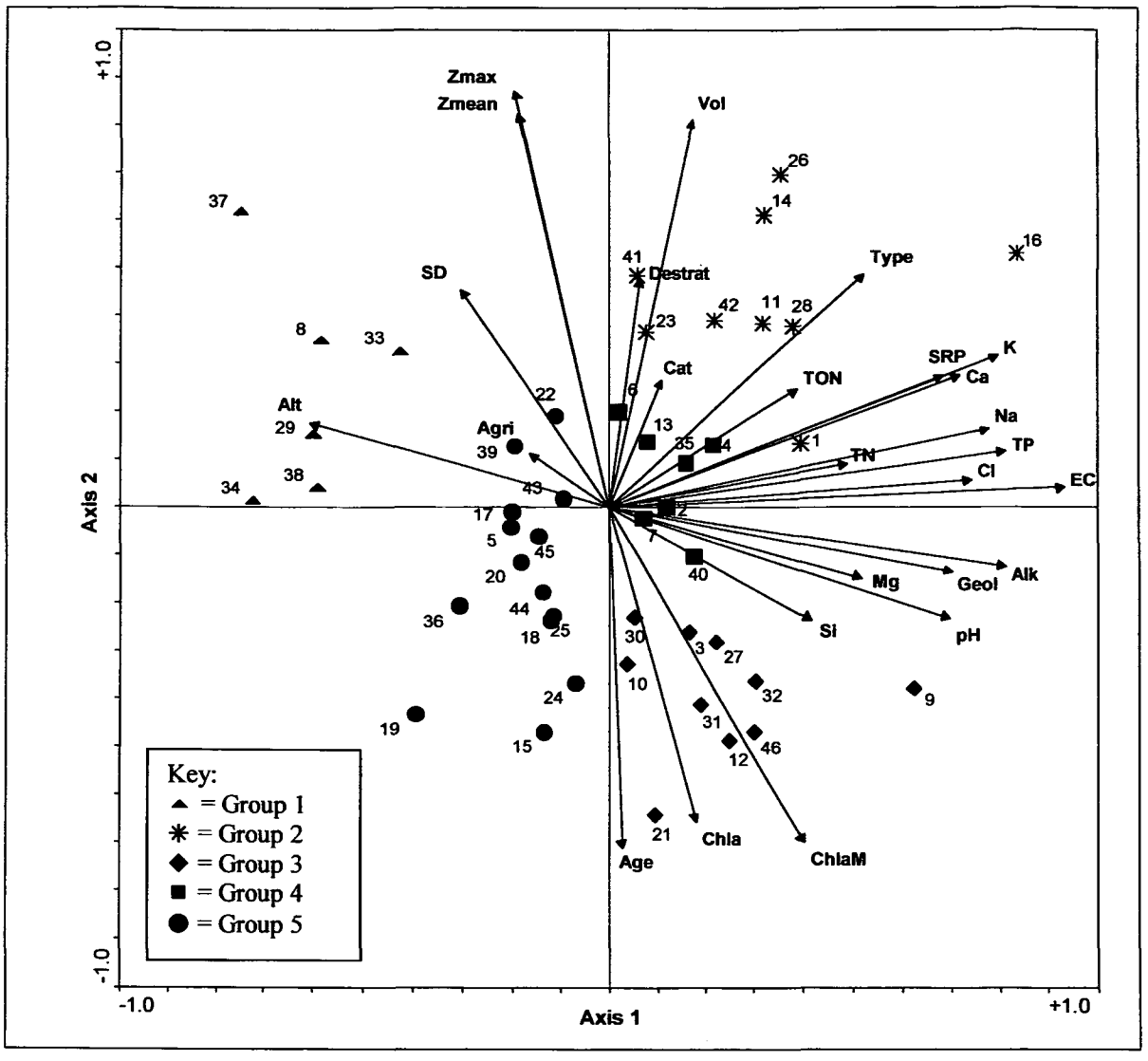


Figure 4.11 Cluster analysis dendrogram illustrating the results of Ward's minimum variance clustering performed on the PCA axes scores (first 2 axes) of the 46 sites and 26 environmental variables (S1 – S46 are the site codes).



Figures 4.12 PCA ordination bi-plot (axis 1 vs. 2) for 46 sites and 26 environmental variables. Sites are grouped according to the results of cluster analysis calculated using PCA axis scores (axes 1 and 2).

Group 1 Sites 8, 29, 33, 34, 37 and 38 are most dissimilar from the other sites in the dataset and make up group 1. These sites are situated in the upper left-hand quadrant of the PCA ordination plot and are characterised by base-poor catchment geology, low pH, alkalinity and conductivity (and its associated ions), low levels of dissolved silica, nutrients and algal productivity, but all lie at relatively high altitudes, have high maximum depths and high water transparencies.

Group 2 The second division in the cluster diagram separates sites 1, 11, 14, 16, 23, 26, 28, 41 and 42. These are situated in the upper right-hand quadrant of the PCA ordination plot and are mainly pump-storage reservoirs of large capacity. Their catchment geology is fairly base-rich, they have moderate to

high pH, alkalinity, EC (and associated ions) and nutrient concentrations, and higher than average water clarity.

Group 3 Sites 3, 9, 10, 12, 21, 27, 30, 31, 32 and 46 form group 3. These sites are situated in the lower right-hand quadrant of the ordination diagram and are largely low capacity, relatively shallow, turbid, highly productive reservoirs. These sites are also older than average, have higher than average nutrient concentrations, pH, alkalinity and EC (and associated ions) and are situated in intermediate to base-rich catchments with moderate to high percentage agricultural land-use. The majority of these reservoirs are of the impounding type with natural catchments of moderate to large size.

Group 4 These sites are located slightly to the right of middle on the ordination plot and include sites corresponding to 'average' characteristics in the dataset in terms of the measured environmental variables. Sites in this group are 2, 4, 6, 7, 13, 35 and 40.

Group 5 This is a large group of sites that could possibly be divided into two separate groups at the next division on the cluster dendrogram. However to avoid over-classification, the integrity of this group has been retained. It includes sites 5, 15, 17, 18, 19, 20, 22, 24, 25, 36, 39, 43, 44 and 45. Most of these sites occupy the lower left quadrant of the ordination plot and are characterised by lower than average EC (and associated ions) and nutrient concentrations, low to moderate pH but moderate to high algal productivity. These reservoirs are generally older than average, of moderate to shallow depth and are of the impounding type, lying in catchments dominated by intermediate geology.

4.5.4 Removal of outliers

Large ecological datasets usually contain (i) redundancies in environmental information, (ii) unusual samples, and (iii) environmental variables which do not determine diatom distributions (Hall & Smol, 1992). Although possible redundancies in environmental information have been explored in this chapter, it has been decided that it is inappropriate at this stage to remove any variables until the environmental and species data have been combined in a direct gradient analysis. Until the influence of the measured environmental variables on the species data have been explored, decisions as to which of the inter-

correlated variables to remove are difficult because of their unknown relative influences on determining species distributions. However, the information gleaned in this exploratory chapter on the extent of inter-correlation between environmental variables will be carried forward to the next chapter, facilitating decisions as to which environmental variables can be made redundant.

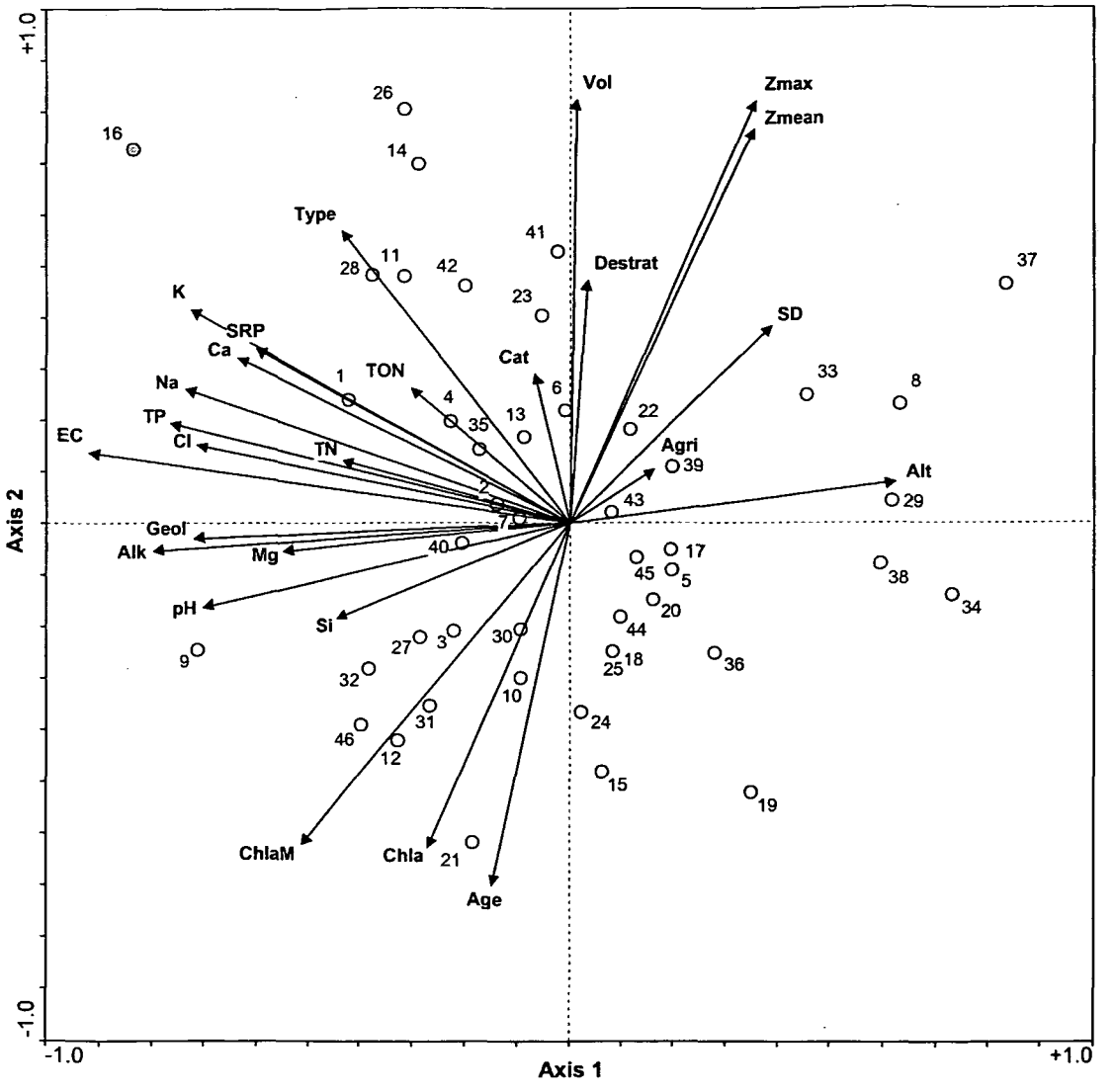


Figure 4.13 PCA ordination biplot illustrating axis 1 vs axis 2 with 45 active sites and 26 environmental variables. (Site 16 is included on the diagram but was made passive in the analysis).

PCA analysis has been used in the current study as a screening exercise to identify outlying sites with unusual or extreme water chemistry / physical characteristics. Outliers can profoundly influence multivariate analyses, usually compressing the important variation into a small area of the available ordination space whilst their own unique variation is highlighted. As ordination techniques aim to underline trends as opposed to emphasizing uniqueness, outliers do little to serve the overall expression of variability within the dataset.

One significant outlier was exposed – site 16 (Grafham). This site was revealed to be an outlier both upon examination of the PCA ordination plot 'by eye' (Figures 4.10a/b), through cluster analysis (Figure 4.11), and by numerous outlier analysis methods applied in PC-Ord 4 (McCune & Mefford, 1999).

Axis	Eigenvalue	Cumulative % variance
1	0.289	28.9
2	0.179	46.8 (17.9)
3	0.099	56.7 (9.9)
4	0.075	64.2 (7.5)

Table 4.9: Results of PCA analysis on 45 sites (site 16 made passive) and 26 environmental variables (numbers in parentheses are individual axes contributions).

Removal of site 16 reduces the environmental dataset to 45 sites and 26 variables. The tabulated results of a PCA analysis run using this reduced dataset can be seen in Table 4.9 and illustrated in Figure 4.13. It can be seen that the resultant ordination bi-plot of axis 1 vs axis 2 is very similar to that illustrated in Figure 4.10a, indicating that the removal of site 16 does not significantly alter the positions of sites on the ordination diagram and scarcely affects the orientation, length and relative positions of the bi-plot arrows. However the results in Table 4.9 reveal that the overall percentage of total variance explained by the first four axes is lower than that explained when all 46 sites are included in the ordination (64.2% as opposed to 65.6%). The percentage variance explained by axis 1 is 1.2% lower than that explained in a PCA with all 46 sites included. The same also holds true for the variance explained by axis 2. (Table 4.9).

4.6 Summary points

- Measured environmental data from the 46 reservoirs in this study were highly comparable with Water Company monitoring data, but failed to capture pronounced, short-lived seasonal trends.
- Mean annual TP concentrations in the dataset reservoirs range from 11-625 μgl^{-1}, with half of all sites having TP in the range 31-100 $\mu gl^{-1}$and thus classified as eutrophic according to OECD (1982) criteria.
- Mean annual Chla concentrations in the dataset reservoirs range from 1.8-25.5 μgl^{-1}. Most reservoirs have Chla concentrations in the range 2.5-8.0 μgl^{-1}, classifying them as mesotrophic according to OECD (1982) criteria. There is thus a discrepancy between trophic state classifications made using TP and Chla measurements.

- Almost all reservoirs in the current study appear to be P limited, however some sites demonstrate seasonally low TN:TP ratios that may indicate N limitation at these times.
- Most water chemistry variables show seasonal trends of varying degrees of amplitude, although EC, Alk and pH show only minor seasonal variation. TP, SRP, TN, TON and Si show peak concentrations in the winter and early spring during periods of autochthonous and allochthonous recharges accompanied by low phytoplankton productivity. Chla concentrations peak in the mid-late summer, reflecting high algal productivity and biomass at this time. SD is highest in the early summer, water clarity appearing to be reduced in summer by algal turbidities and in winter by non-algal particulates.
- Relationships between nutrient concentrations and algal productivity are not as strong for reservoirs in the current study as have been reported for natural lakes. Similarly, relationships between water clarity and algal productivity are less strong than reported for natural lakes. The relationship between TN and TP was statistically significant, but only weak. TP appears to be partially related to catchment geology.
- Results of PCA ordination showed that the main axis of variation in the environmental dataset was related to the combined influence of pH, alkalinity, conductivity (and its associated ions) and nutrients.
- The second axis of variation in the environmental data was related to algal productivity and water clarity.
- One site, Grafham (site 16), was identified by cluster analysis as a clear outlier in terms of its extreme water chemistry (e.g. annual average SRP and TP concentrations more than double those of any other site). This site has been removed from the environmental dataset.

CHAPTER FIVE

Calibration set species data and species-environment relations

5.1 Introduction

This chapter presents the results of both indirect (Detrended Correspondence Analysis (DCA)) and direct gradient analysis (Canonical Correspondence Analysis (CCA)) techniques used to explore patterns of variation in the diatom species data from surface sediment assemblages and seasonal plankton samples. The overall aim of this chapter is to gain an understanding of diatom species-environment relationships and diatom ecology in U.K. lowland reservoirs with a view to the development of paleolimnological inference models for these sites.

Initially the full surface-sediment diatom species dataset is examined for general trends. This dataset is then investigated for patterns of floristic variation using DCA. The major axes of variation in the species data are described and summarised with suggestions as to the potential factors determining species distributions. CCA methods are then utilised to assess the statistical significance of species-environment relationships, enabling determination of the measured environmental factors most strongly correlated with species distributions, thus demonstrating potential for the subsequent development of inference models.

Planktonic diatom species were dominant in the surface sediments of the calibration set reservoirs and it is envisaged that inference models based on 'planktonic' species alone could feasibly be created. To investigate the potential of this idea, the dataset was reduced to surface sediment 'planktonic' taxa only and again patterns of variation in the species-only and species-environment datasets are explored using DCA and CCA respectively.

5.2 The full site, species and environmental variable dataset

5.2.1 General observations on surface sediment diatom data (all species)

A total of 208 diatom taxa were identified to species level in the surface sediments of the 46 reservoirs. Only 0.02% of diatom valves counted were unassigned to a species. Table 5.1 shows that the total number of taxa recorded in a single surface sediment sample ranged from 16 in site 3, which was dominated by *F. crotonensis*, to 61 taxa in site 35, in which no single taxon exceeded a relative frequency of 10%. The mean number of species per site

Site code	Total number of taxa	Total valve count	Floristic diversity
1	50	473	0.11
2	29	565	0.05
3	16	715	0.02
4	29	554	0.05
5	26	389	0.07
6	56	526	0.11
7	30	454	0.07
8	26	542	0.05
9	61	590	0.10
10	34	1129	0.03
11	22	489	0.04
12	44	500	0.09
13	33	320	0.10
14	49	532	0.09
15	52	425	0.12
16	32	426	0.08
17	38	405	0.09
18	34	585	0.06
19	34	801	0.04
20	40	854	0.05
21	45	597	0.08
22	41	655	0.06
23	50	467	0.11
24	22	437	0.05
25	26	445	0.06
26	52	559	0.09
27	46	650	0.07
28	48	483	0.10
29	26	260	0.10
30	28	601	0.05
31	45	510	0.09
32	46	640	0.07
33	35	470	0.07
34	48	726	0.07
35	61	464	0.13
36	26	409	0.06
37	26	581	0.04
38	34	544	0.06
39	30	512	0.06
40	51	508	0.10
41	43	472	0.09
42	43	409	0.11
43	42	541	0.08
44	29	361	0.08
45	46	590	0.08
46	41	621	0.07
Mean	38	539	0.07
Median	39	519	0.07
Min	16	260	0.02
Max	61	1129	0.13
SD	11	146	0.02

Table 5.1 Summary statistics for the surface sediment diatom samples. Total number of taxa recorded in each sample, the total valve count and the ratio of diatom taxa to valves counted (floristic diversity).

was 38 (± 11). Floristic diversity across the dataset was moderately variable, ranging from 0.02 in site 3 to 0.13 in site 35 (mean 0.07 ± 0.02). Thirty-five sites had a diversity score of 0.10 or less, reflecting the predominance of one or two taxa. This can be expected in lowland reservoirs where depth is often sufficient to provide an extensive pelagic environment for the development of species-poor 'blooms' of planktonic taxa, but the water clarity is usually insufficient to enable the extensive development of a more diverse periphytic flora.

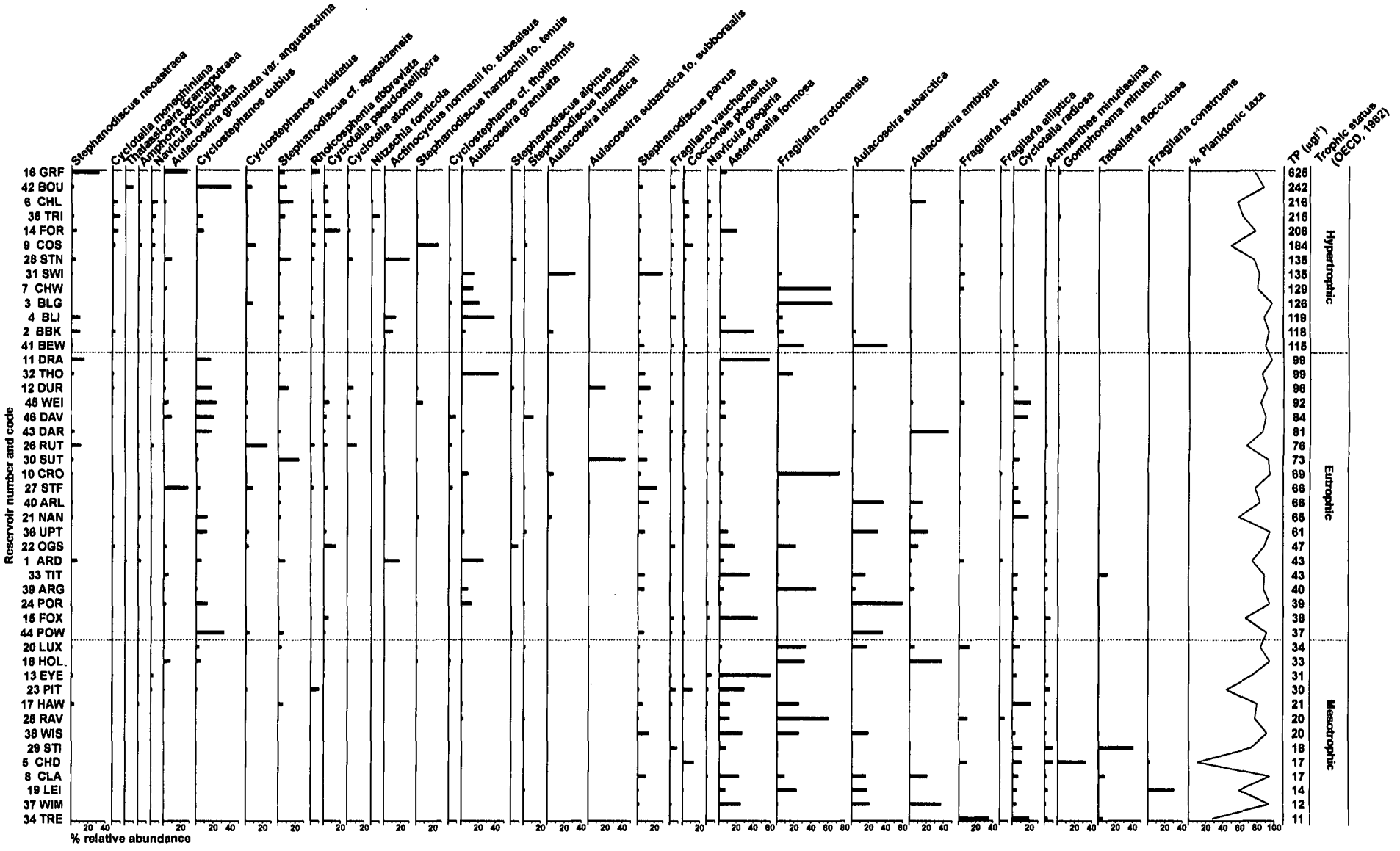


Figure 5.1 Percentage relative abundances of selected diatom taxa in the surface sediments of the 46-reservoir calibration dataset. Sites are ordered from highest to lowest mean annual TP and are classified according to trophic status, using OECD (1982) TP criteria (only taxa occurring with ≥5% relative abundance in one or more samples are shown).

Figure 5.1 illustrates the dominant (>5% in any one site) diatom taxa present in the surface sediment samples of the 46 reservoirs. Sites are ordered from highest to lowest measured annual mean TP concentration and OECD (1982) trophic classes are overlaid for reference. Sites classified as hypertrophic are characterised by the presence of *Actinocyclus normanii* fo. *subsalsus*, *Cyclotella meneghiniana*, *Stephanodiscus neoastraea*, *Stephanodiscus* cf. *agassizensis* and *Aulacoseira granulata*. Sites classified as eutrophic are characterised by *Aulacoseira subarctica*, *Aulacoseira ambigua*, *Cyclotella radiosa*, *Cyclostephanos dubius*, *Aulacoseira subarctica* fo. *subborealis*, *A. granulata* and *Aulacoseira granulata* var. *angustissima*. Sites classified as mesotrophic are characterised by *A. subarctica*, *A. ambigua*, *C. radiosa*, *Tabellaria flocculosa*, *Achnanthes minutissima* and small *Fragilaria* spp. *Stephanodiscus parvus*, *Fragilaria crotonensis* and *Asterionella formosa* occur across the full range of trophic categories. In sites where it is present, *F. crotonensis* occurs at high percentage relative abundances and it is not observed in sites with TP concentrations >150 μgl^{-1}. *A. formosa* occurs at highest overall percentage relative abundance in mesotrophic sites and in eutrophic sites with TP concentrations <65 μgl^{-1}.

5.3 Detrended Correspondence Analysis (DCA): All sites and species.

DCA was used to reveal major patterns of variation in the surface sediment diatom species data. The DCA analysis used in this study was based on detrending by segments and non-linear rescaling (Hill & Gauch, 1980). Rare taxa (i.e. taxa with percentage abundances less than one fifth of the most common taxon) were down-weighted in proportion to their frequency (ter Braak & Šmilauer, 1998b). Diatom taxa were included in ordinations if they were a) determined to species level and b) present in a minimum of two reservoirs, achieving ≥1% relative abundance in at least one site (see Chapter 3 for reasoning). After removing taxa that failed to fulfil these selected criteria, the dataset consisted of 94 taxa from 46 sites. The full taxon names / authorities and taxon abbreviations for the 94 dominant taxa are listed in Appendix 3.

Initially, DCA analysis was performed on the full dataset (94 taxa and 46 sites). The results are presented in Table 5.2 As is typical for noisy datasets with many zero values (Jongman *et al.*, 1995), the first two axes of the DCA ($\lambda_1 = 0.492$; $\lambda_2 = 0.347$) account for only 18.8% (11.0% and 7.8% respectively) of the variation in the diatom species data. Community variation, as indicated by the lengths of the species gradients (2.938 and 3.342 standard deviation units respectively), covers a relatively large range and indicates that most species responses would be approximated by unimodal response models (Jongman *et al.*, 1995). This supports the choice of DCA ordination for the species data and indicates that unimodal

(D)CCA ordination methods are suitable for subsequent analysis of species-environment relationships (ter Braak & Prentice, 1988; ter Braak & Šmilauer, 1998b).

Axis	Eigenvalue	Length of gradient (SD units)	Cumulative variance represented (%)
1	0.492	2.938	11.0
2	0.347	3.342	18.8 (7.8)
3	0.251	2.411	24.4 (5.6)
4	0.196	2.050	28.8 (4.4)

Table 5.2 Results of DCA analysis on the 94 common taxa in the surface sediments of 46 reservoirs (numbers in parentheses are individual axes contributions).

Figures 5.2a and 5.2b display the results of DCA on the full dataset of 94 species and 46 sites. It is clear from this analysis that sites 5 (Cheddar), 29 (Stithians) and 34 (Trenchford) are clearly distinct from the other sites in terms of their diatom assemblages. The diatom taxa in the lower portion of the graph (0 to -2.5 on the y axis) are predominantly associated with these sites. The locations of these species on the ordination diagram are determined by their high relative abundances at these sites. Species such as *Gomphonema minutum*, *Pseudostaurosira brevistriata, T. flocculosa*, *Eunotia minor*, *Anomoeoneis vitrea*, *Nitzschia perminuta* and *Encyonema gracile* were present in one or more of sites 5, 29 and 34. These species are either characteristic of clean, clear-water environments (of varying trophic status), where periphytic taxa can dominate the assemblage e.g. *P. brevistriata* and *G. minutum*, or, as in the case of *T. flocculosa*, *E. minor*, *A. vitrea, N. perminuta* and *E. gracile*, considered indicators of electrolyte poor, oligotrophic, circumneutral to slightly acidic waters. The occurrence of these species in sites 5, 29 and 34 supports this premise, since these sites are consistent with the above descriptions.

5.3.1 Removal of outliers

Owing to the high scores on axis 2 for sites 5 (Cheddar), 29 (Stithians) and 34 (Trenchford), the scaling concentrates the remaining samples into a smaller area of the plot. This results in wasted ordination space and inadequate expression of total variability across the dataset. Sites 5, 29 and 34 were therefore made passive and the DCA re-run with a reduced dataset of 43 sites and 83 species. Several species were removed because they failed to meet the aforementioned abundance criteria (see section 5.2.2) when the three outliers were excluded. Table 5.3 and Figures 5.3a and 5.3b illustrate the results.

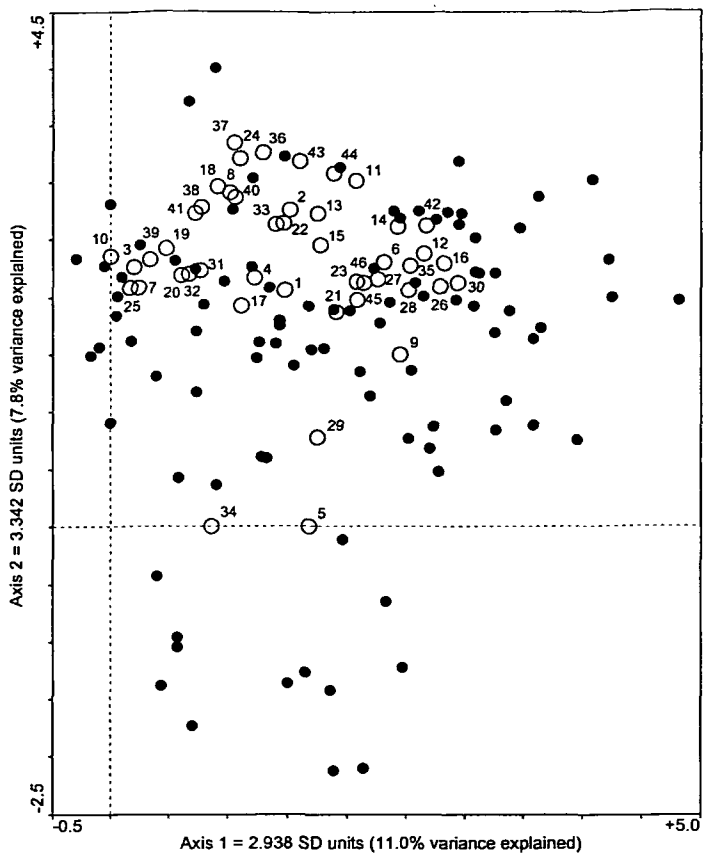
Axis	Eigenvalue	Length of gradient (SD units)	Cumulative variance represented (%)
1	0.492	2.917	13.2
2	0.324	2.586	21.9 (8.7)
3	0.206	2.389	27.4 (5.5)
4	0.147	1.729	31.3 (3.9)

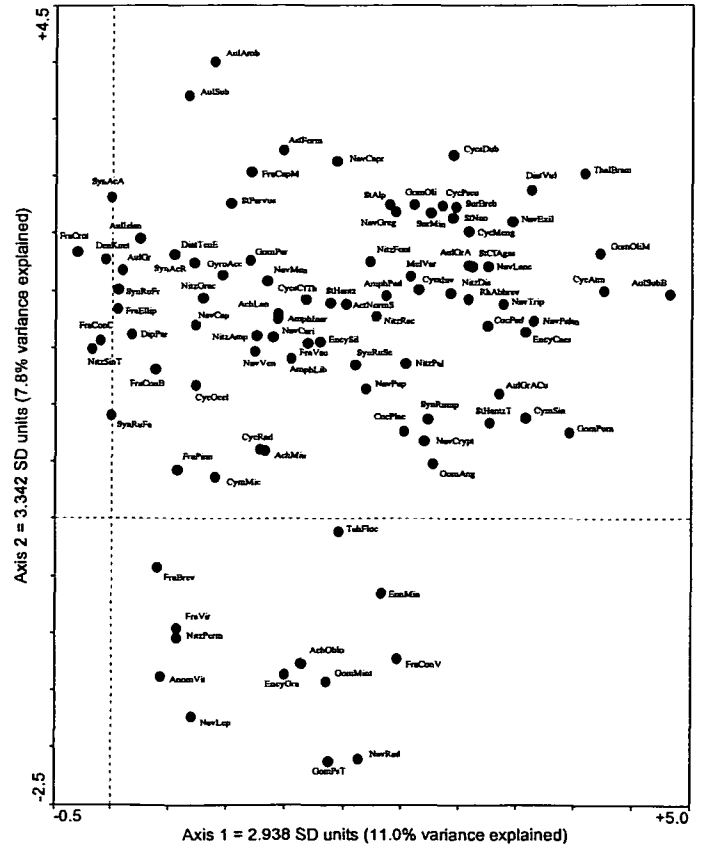
Table 5.3 Results of DCA on the 83 common taxa in the surface sediments of 43 sites (numbers in parentheses are individual axes contributions).

The results both before (Table 5.2 and Figures 5.2a and 5.2b) and after (Table 5.3 and Figures 5.3a and 5.3b) removal of outliers from the ordination are largely similar both statistically and graphically. However, because sites 5, 29 and 34 had a relatively large influence on axis 2, their removal reduced the eigenvalue for the second axis, decreased the length of axis 2's gradient from 3.482 to 2.586, and consequently increased the proportion of the cumulative variance in the species data captured by axis 1 (from 11% to 13.2%). Following removal of outliers, the gradient lengths of both DCA axis 1 and 2 are still sufficient to assume unimodal responses for most of the species and hence the use of unimodal models i.e. (D)CCA for subsequent direct gradient analyses (ter Braak & Prentice, 1988; ter Braak & Šmilauer, 1998b).

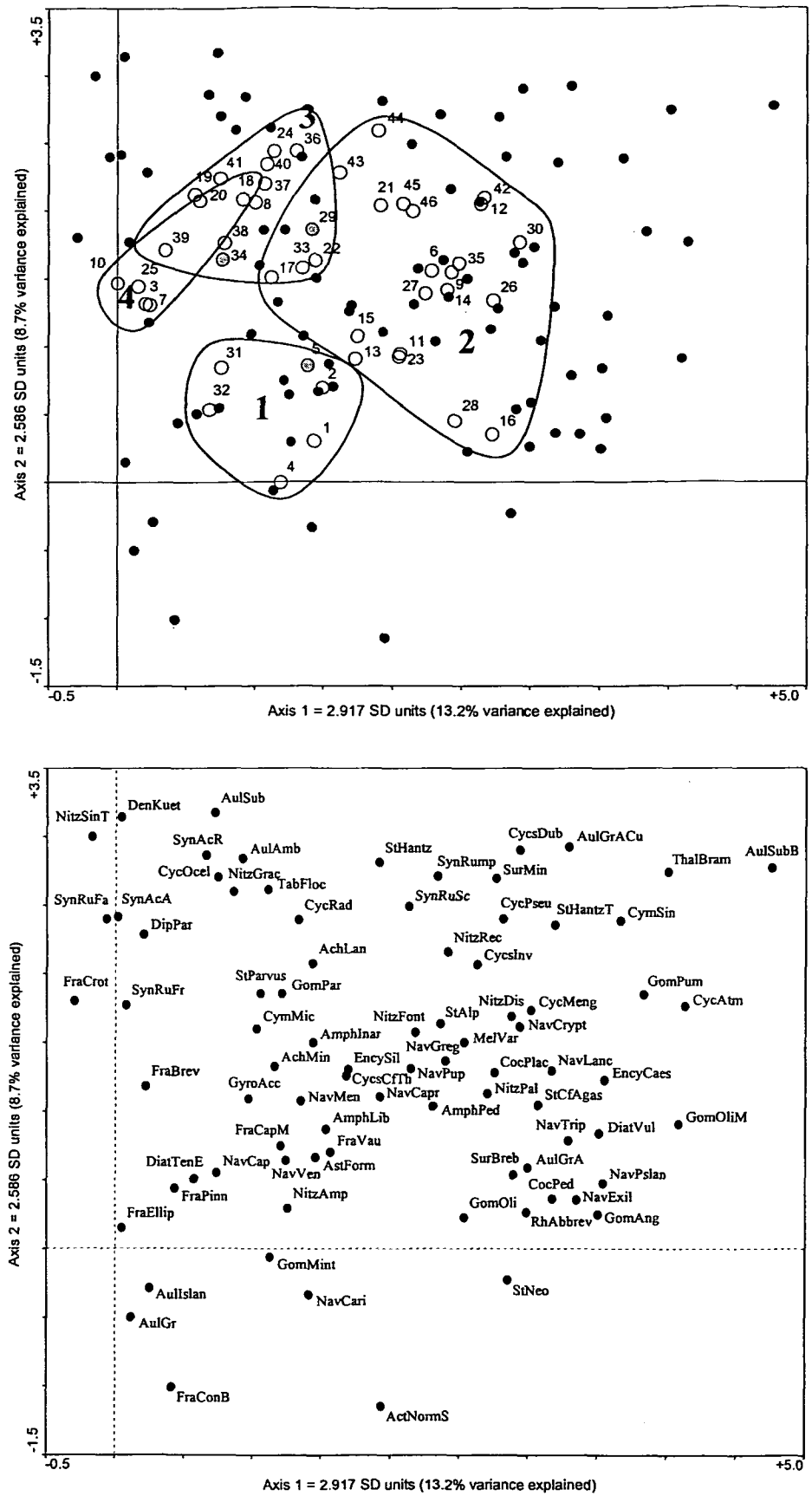
The species removed from the analysis were *Achnanthes oblongella*, *A. vitrea*, *E. gracile*, *E. minor*, *Staurosira construens* var. *construens*, *Staurosira construens* var. *venter*, *Fragilaria virescens*, *Gomphonema pseudotenellum*, *Navicula leptostriata*, *Navicula radiosa* and *N. perminuta*. These species are typically reported as 'non-planktonic' taxa, although they may be epiphytic on other algae living in the plankton (Round, 1998). Since elimination of these 'non-planktonic' taxa reduces the length of axis 2, it is thought that axis 2 reflects habitat or life-form, determined perhaps in part by water clarity.

Overlain on Figure 5.3a are hulls delineating the 43 sites into four groups according to the results of a TWINSPAN classification on their species' assemblages. It is clear that there is some degree of overlap in the groupings, indicating that the diatom species found in the surface sediments of sites classified into different groups are not entirely distinct. This is unsurprising, because although the reservoirs are modified environments, they still exhibit continuous variation across the dataset and thus cannot easily be delineated into groups. Poor site groupings may further arise because both periphytic and planktonic diatom species are included in the classification, with many periphytic species occurring across the dataset but often at low relative abundance. Overall however it appears that the groupings are driven by the dominant planktonic taxa. Group 1 is the most distinct, largely characterised





Figures 5.2a and 5.2b **Ordination biplots illustrating the results of DCA analysis on the full dataset of 94 species and 46 sites (open circles = sites and black circles = species). 5.2a displays both sites and species, 5.2b displays species only. (See Appendix 3 for conversion of codes to full species names).**



Figures 5.3a and 5.3b. **Ordination biplots illustrating the results of DCA analysis on the reduced dataset of 83 species and 43 sites (open circles = sites and black circles = species). Sites made passive in the analysis (sites 5, 29 and 34) are shaded. Groups determined by TWINSPAN classification. (See Appendix 3 for conversion of codes to full species names).**

by sites containing *A. granulata* and *Aulacoseira islandica*. Group 2 is the largest and most diverse cluster spanning a considerable area of the DCA ordination plot. Species typically found in reservoirs of this group include *S. neoastraea*, *S.* cf. *agassizensis* and *Cyclostephanos dubius*, with *C. radiosa* occurring in a cluster of sites within this group. Group 3 is overlapped by both Group 2 and Group 4, possibly driven by the joint occurrence of *A. ambigua* across these groups. Group 3 sites are also characterised by *A. subarctica* and to some extent *T. flocculosa*. Group 4 overlaps with Group 3 and its delineation appears to be driven predominantly by those sites containing large percentages of *F. crotonensis*. Both Groups 3 and 4 appear to contain a large number of pennate taxa including *Synedra acus* var. *angustissima*, *Synedra rumpens* (inc. var. *familiaris* and var. *fragilarioides*), *T. floccuolosa*, *F. crotonensis* and *Nitzschia gracilis*.

The groupings derived exclusively from the species data (Figure 5.3a) are broadly similar to those determined solely by the environmental data in Figure 4.12, indicating that although there appear to be relationships between the measured environmental variables and diatom species assemblages, they may not be easy to interpret. Species-environment relationships will be explored further, using canonical correspondence analysis ordination techniques, in the following section.

5.4 Canonical Correspondence Analysis (CCA): All sites and species

5.4.1 Data screening prior to the application of CCA

CCA is a direct gradient analysis technique used to explore relationships between diatom species' distributions and measured environmental variables. This ordination method assumes that the relationship between species and environmental variables is unimodal. The implementation of CCA is supported by the resultant gradient lengths (2.917 and 2.586 SD units respectively for DCA axes 1 and 2) of earlier DCAs (Table 5.3), indicating that most species responses are best approximated by unimodal response models (Jongman *et al.*, 1995).

Large ecological datasets contain redundancies in environmental information, unusual samples and environmental variables that do not determine diatom distributions (Hall & Smol, 1992). The site, species and environmental datasets were subjected to initial screening during PCA (section 4.5) and DCA (section 5.3.1). These methods isolated Grafham (site 16) as an outlier in terms of its unusual water chemistry, and Cheddar (site 5), Stithians (site 29) and Trenchford (site 34) as outliers in terms of their atypical species

assemblages. These sites were removed prior to CCA analyses, resulting in a dataset of 42 sites, 83 species and 26 environmental variables.

5.4.2 Initial CCA applied to the full, screened dataset.

An initial exploratory CCA (with downweighting of rare species) was run on the full, screened dataset of 42 sites, 83 species and 26 environmental variables. The results are presented in Table 5.4 and Figure 5.4. CCA axis 1 (λ_1 = 0.358) and axis 2 (λ_2 = 0.324) together explain 18.8% (9.9% and 8.9% respectively) of the cumulative variance in the full diatom dataset. The correlations between the species and environmental variables are high for axis 1 (0.925) and axis 2 (0.910) and the 26 variables together explain 67.7% of the variance in the diatom data, indicating a strong relationship between the measured environmental variables and the 83 diatom species. CCA eigenvalues, particularly that of axis 1, are less than those seen for DCA of the diatom data alone (λ_1 = 0.486, λ_2 = 0.338). Since the DCA axis 1 eigenvalue reflects the maximum separation of the species data, this suggests that the measured environmental variables have a moderately significant influence over diatom species assemblage composition and that the environmental data express the main ecological gradients reasonably well. However, an assessment of the significance of the first canonical axis is statistically insignificant (P = 0.49 with 999 Monte Carlo permutations), indicating that there is no single dominating gradient determining the relation between the diatom species and measured environmental variables. This result may be an artefact of the inclusion in the CCA of too many intercorrelated environmental variables. As redundant inter-corelated variables are eliminated, the significance was expected to increase.

Axis	Eigenvalue	Species / environment correlation	Cumulative % variance (species)	Cumulative % variance (species / environment)	Sum of all unconstrained eigenvalues	Sum of all canonical eigenvalues
1	0.358	0.925	9.9	14.6		
2	0.324	0.910	18.8 (8.9)	27.8 (13.2)		
3	0.293	0.909	26.9 (8.1)	39.7 (11.9)		
4	0.224	0.947	33.1 (6.2)	48.8 (9.1)		
					3.630	2.459

Table 5.4 Results of CCA on the 83 diatom species with 42 active sites and 26 environmental variables (numbers in parentheses are individual axes contributions).

A large number of the measured environmental variable vectors lie close together on the ordination plot (Figure 5.4). This further illustrates the high degree of inter-correlation

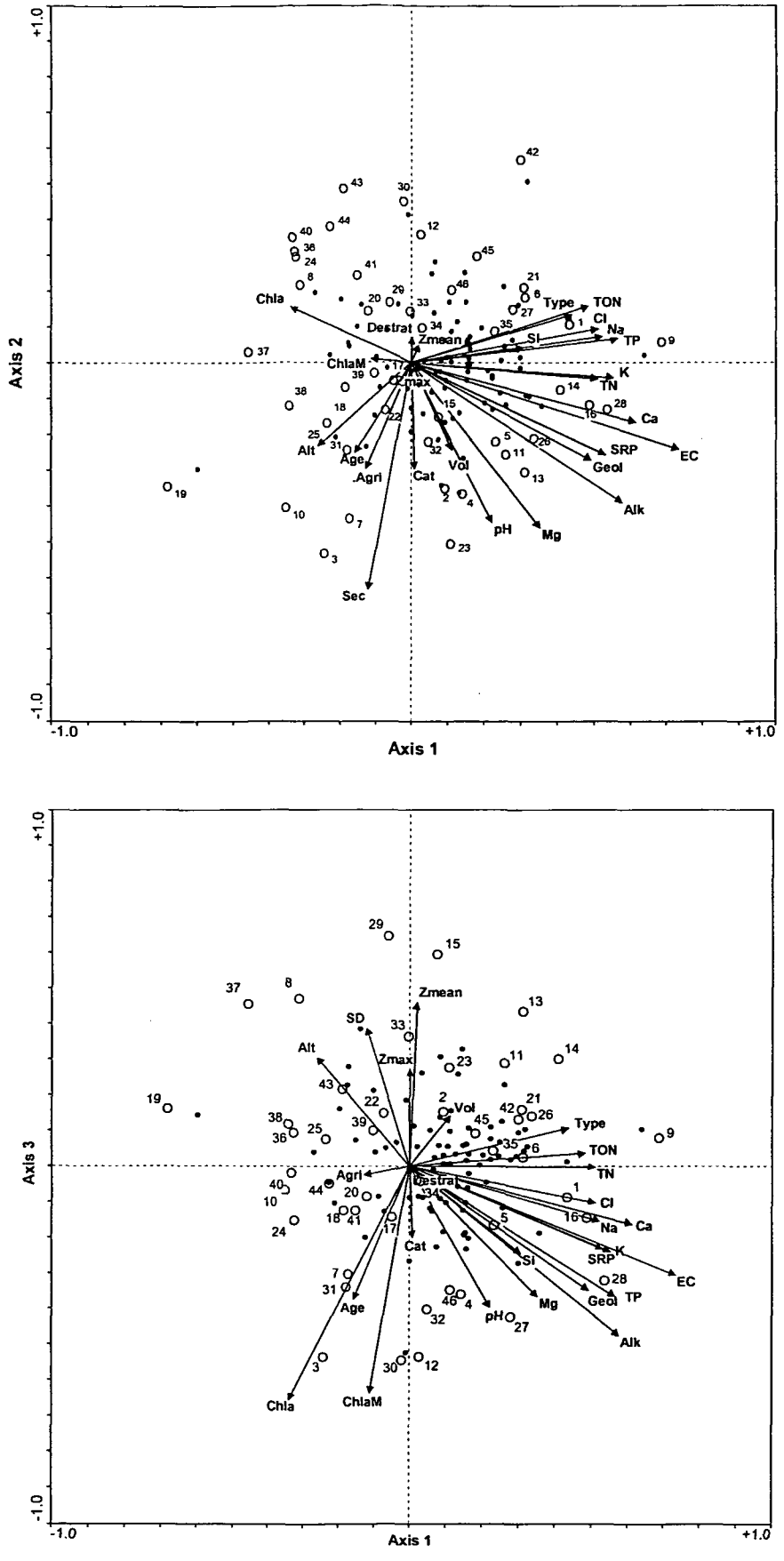


Figure 5.4a/b CCA triplots illustrating 26 environmental vectors and 83 diatom species from 42 sites (environmental vectors are labelled, sites are numbered, but species (black circles) are not named for clarity). 5.4a illustrates axis 1 vs. 2. 5.4b illustrates axis 1 vs. 3.

between many of the measured environmental variables, as highlighted in section 4.4. Most variables are associated with axis 1. For example conductivity (EC) (and its associated ions), alkalinity (Alk), the nutrients total phosphorus (TP), soluble reactive phosphorus (SRP), total nitrogen (TN) and total oxidised nitrogen (TON), and to a lesser extent Silica (Si) are all positively correlated with axis 1. This indicates that this axis differentiates sites according to both dissolved ion concentration and nutrients. Secchi depth (SD), pH and Magnesium (Mg) appear to be negatively correlated with axis 2, signifying that this axis is partially related to dissolved ion concentration and type, but that since the most influential variable on this axis is SD, axis 2 is predominantly a reflection of water clarity. Mean chlorophyll-a (Chla), maximum chlorophyll-a (ChlaM), and to a lesser extent reservoir age (Age) are all negatively correlated with axis 3, and mean depth (Z_{mean}), maximum depth (Z_{max}) and SD are positively correlated with this axis, indicating that axis 3 is negatively related to water clarity, which in turn is negatively related to algal biomass. The strength of influence of the major ion, nutrient and water clarity variables is not surprising, since numerous studies have documented changes in diatom community composition along these gradients (e.g. Fritz, 1989; Bennion *et al.* 1996; Bradshaw 2001).

5.4.3 Selection of environmental variables for inclusion within CCA

The literature on the process of selection of environmental variables for inclusion or exclusion in CCA is extremely unclear, and as a result remains an essentially subjective process (Kent, unpublished). ter Braak & Šmilauer (1998) recommend that a small number of carefully selected variables is preferable to the inclusion of a large number of poorly chosen ones. This is because variables are often highly intercorrelated, providing no unique contribution to the ordination and thus exaggerating the results of the final CCA. Following the principle of parsimony in statistics (Birks, 1998), the subsequent data screening exercises were carried out to eliminate both redundancies in environmental information and environmental variables showing only a weak relationship with diatom distributions.

5.4.4 Intercorrelation between environmental variables

An initial assessment of the intercorrelation between environmental variables was obtained by examination of the Pearson's correlation matrix between all 26 variables. This is presented and discussed in Section 4.4.1 (Table 4.6). The main observation was that considerable intercorrelation exists between the environmental variables, providing opportunities for the reasoned removal of redundant variables flagged-up in ensuing data screening exercises.

5.4.5 Constrained CCAs

Constrained CCAs were run for each individual environmental variable (ter Braak & Šmilauer, 1998b). In this way, species composition was constrained to each variable in turn to establish its ability to explain a statistically significant amount of variance in the species data.

Variable	% species variance	Constrained CCA			
		λ_1	λ_2	λ_1/λ_2	p value
Alk	7.1	0.259	0.486	0.533	0.001
EC	7.0	0.254	0.478	0.531	0.001
Chla	5.7	0.207	0.469	0.441	0.001
TP	5.5	0.200	0.474	0.422	0.002
SD	5.4	0.196	0.468	0.419	0.001
Mg	5.5	0.199	0.485	0.410	0.002
SRP	5.2	0.189	0.483	0.391	0.003
K	5.1	0.184	0.472	0.390	0.003
Geol	5.0	0.182	0.486	0.374	0.003
Ca	4.8	0.174	0.475	0.366	0.005
Na	4.7	0.170	0.463	0.367	0.007
Cl	4.5	0.164	0.459	0.357	0.008
Type	4.2	0.153	0.449	0.341	0.014
ChlaM	4.2	0.153	0.474	0.323	0.011
Age	3.9	0.142	0.450	0.316	0.022
pH	4.1	0.150	0.479	0.313	0.021
TON	3.8	0.137	0.448	0.306	0.046
Alt	3.7	0.133	0.478	0.278	0.065
TN	3.4	0.123	0.466	0.264	0.082
Z_{mean}	3.4	0.123	0.479	0.257	0.098
Agri	3.1	0.111	0.477	0.233	0.178
Cat	3.0	0.110	0.481	0.229	0.182
Si	2.7	0.099	0.481	0.206	0.307
Z_{max}	2.7	0.099	0.484	0.205	0.302
Vol	2.7	0.099	0.486	0.204	0.317
Destrat	2.0	0.074	0.486	0.152	0.724

Table 5.5 Results of constrained CCA analyses for all 26 environmental variables. Variables are ranked according to their strength of influence over diatom assemblages, expressed as the eigenvalue ratio, axis 1 versus axis 2 (λ_1/λ_2). The 17 Variables explaining a statistically significant amount of species variation are shaded.

The series of constrained CCAs identified 17 of the original 26 environmental variables as explaining a statistically significant ($P < 0.05$, using 999 unrestricted Monte Carlo permutations) amount of variation in the diatom data (Table 5.5). These variables each explained between 7.1% and 3.8% of the total species variance. Alk showed the highest λ_1/λ_2 ratio (0.533) in the dataset, followed by EC (0.531), Chla (0.441), TP (0.422), SD (0.419) and Mg (0.410). All other λ_1/λ_2 ratios were <0.4. These results suggest that the above-mentioned variables showed sufficiently strong relationships with diatom species distributions to support generation of inference models. Nine variables (TN, Si, Z_{max}, Z_{mean},

Destrat, Alt, Vol, Cat and Agri) failed to independently influence diatom distributions. These variables have been removed from the subsequent analyses.

Axis	Eigenvalue	Species / environment correlation	Cumulative % variance (species)	Cumulative % variance (species / environment)	Sum of all unconstrained eigenvalues	Sum of all canonical eigenvalues
1	0.345	0.915	9.5	19.2		
2	0.304	0.865	17.9 (8.4)	36.1 (16.9)		
3	0.220	0.829	23.9 (6.0)	48.3 (12.2)		
4	0.196	0.903	29.3 (5.4)	59.2 (10.9)		
					3.630	1.797

Table 5.6 Results of CCA on the 83 diatom species with 42 active sites and 17 environmental variables (numbers in parentheses are individual axes contributions).

With the reduced environmental dataset of 17 variables, both the first canonical axis (P = 0.03) and all canonical axes (P = 0.001) were found to be statistically significant (999 unrestricted Monte Carlo permutations). The eigenvalues, species/environment correlations and cumulative percentage species variance explained by axes 1 and 2 decrease slightly with the removal of the nine environmental variables (Table 5.4 and Table 5.6). However the cumulative percentage variance in the species / environment relationship explained by axes 1 and 2 increases markedly – over a third of the variance is now explained by axes 1 and 2, and almost half is explained by axes 1, 2 and 3 combined. The total explained variance (sum of all canonical eigenvalues) is approximately 73% of that which could be explained by the full suite of 26 environmental variables, indicating that the removal of nine variables retains much of the explanatory power of the ordination.

Figures 5.5a and 5.5b show that the vectors for the remaining 17 environmental variables are related to one another and to the CCA axes in much the same pattern as that shown by the full suite of environmental variables in Figures 5.4a and 5.4b.

5.4.6 Inter-set correlations to assess axes contributions of variables

According to ter Braak & Šmilauer (1998), if the t-value of a variable's canonical coefficient is less than 2.1 in absolute value, then the variable does not contribute much to the fit of the species data in addition to the contributions of the other variables in the analysis. However, since canonical coefficients become unstable when the environmental variables are strongly correlated, it is preferable to examine the stable inter-set correlations

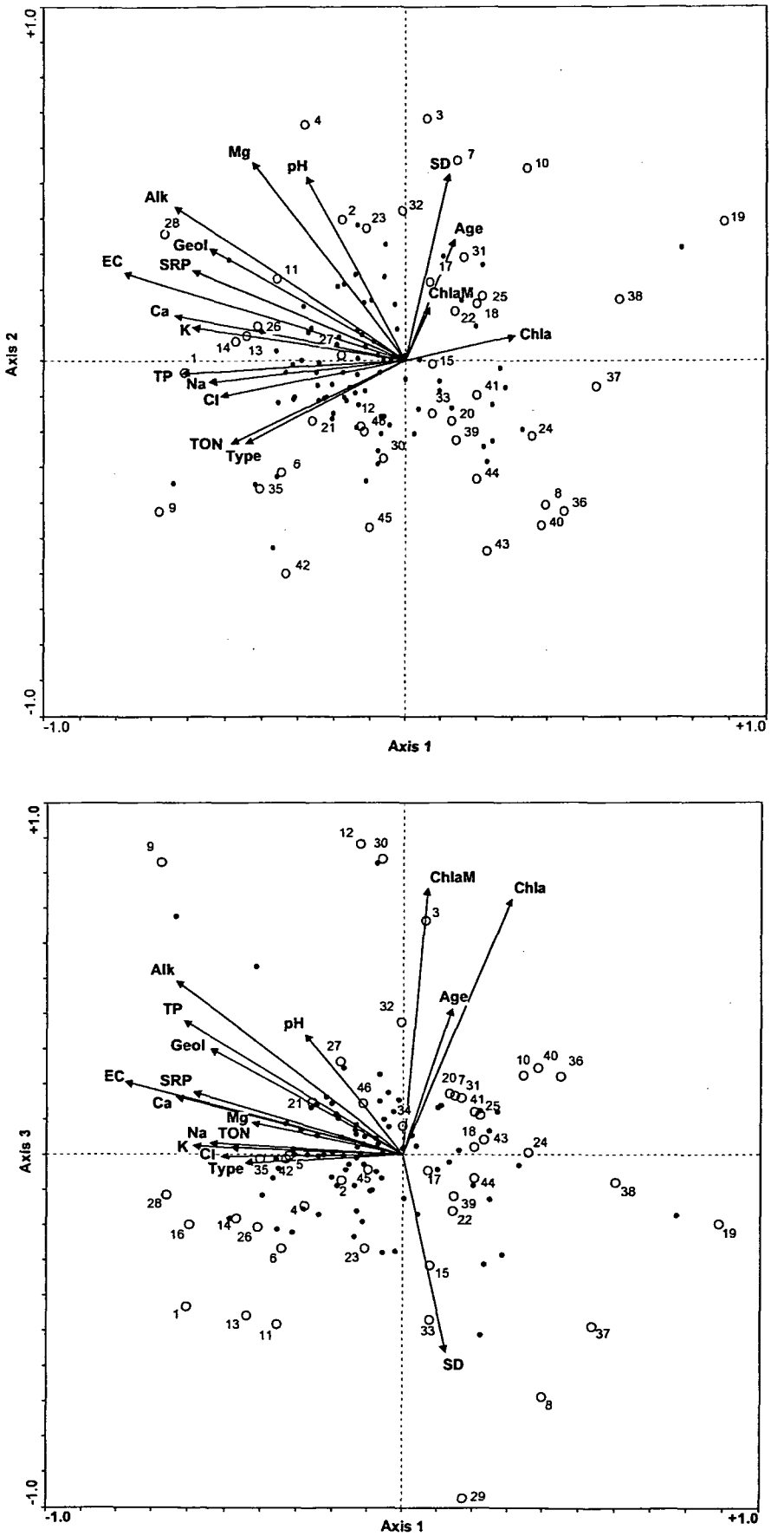


Figure 5.5a/b CCA tri-plots illustrating 17 environmental vectors and 83 diatom species from 42 sites. (Environmental vectors are labelled, sites (open circles) are numbered, but species (black circles) are not named for clarity). 5.5a = Axis 1 vs. 2; 5.5b = Axis 1 vs. 3.

to determine the relationship between environmental variables and axes, particularly where multi-collinearity is known to exist within the environmental dataset.

Based on the inter-set correlation results in Table 5.7, the seventeen environmental variables all contribute significantly to one or more of CCA axes 1, 2 or 3. The inter-set correlation for EC is the largest for axis 1 (-0.71), indicating its dominant influence in explaining diatom species distributions. Alk, Ca, TP, SRP, K, Na, Geol, Cl, TON and Type explain further variance in diatom distributions along axis 1, due to their negative correlations with this axis. The large number of variables with high inter-set correlations on axis 1, in addition to the highly significant correlation coefficients between pairs of these variables (Table 4.6), indicates that many are multicollinear and thus potentially redundant. Mg and pH are positively correlated with axis 2. Chla, ChlaM and Age are positively correlated with axis 3. SD appears to contribute in similar proportions to both axis 1 and 2, being positively correlated with axis 2 (0.45) and negatively correlated with axis 3 (-0.46).

Variable	Inter-set correlation		
	Axis 1	Axis 2	Axis 3
EC	-0.7087	0.2156	0.1705
Alk	-0.5795	0.3738	0.4058
Ca	-0.5790	0.1093	0.1346
TP	-0.5582	-0.0304	0.3135
SRP	-0.5344	0.2199	0.1449
K	-0.5339	0.082	0.021
Na	-0.4938	-0.0529	0.0272
Geol	-0.4920	0.2728	0.2489
Cl	-0.4659	-0.0858	-0.004
TON	-0.4391	-0.2007	0.0169
Type	-0.4045	-0.2015	-0.0201
Mg	-0.3877	0.4806	0.0762
pH	-0.2531	0.4454	0.2803
SD	0.1131	0.4523	-0.4632
ChlaM	0.0632	0.1274	0.6236
Chla	0.2793	0.06	0.6004
Age	0.1283	0.2927	0.3412

Table 5.7 Inter-set correlations between the 17 measured environmental variables selected in constrained CCAs and the first three CCA axes. Shaded boxes indicate the axis to which each variable is most highly correlated.

5.4.7 Partially constrained CCAs (pCCAs)

The results of constrained CCAs (Table 5.5) showed that 17 of the original 26 measured environmental variables exerted a significant independent influence on diatom species distributions. These results, in combination with examination of the Pearson's correlation coefficients (Table 4.6) and the inter-set correlations between these variables and the ordination axes (Table 5.7), were utilised to ascertain variables explaining both significant

independent variation and representing different axes of variation in the species data. These variables were selected as the sole environmental variables for pCCAs. The remaining members of each group of correlated variables were entered in turn as covariables to test their ability to independently influence diatom distributions. Alk, Mg and Chla were chosen as the sole representative environmental variables because each explained the highest percentage variance in individual constrained CCAs (Table 7.5) for each group. The statistical significance of taxon-environment relationships (given the covariables) was assessed using Monte Carlo permutation tests with 999 random permutations. Any variable with $p>0.05$, therefore failed to explain a statistically significant independent influence on diatom distributions and was thus excluded from the subsequent analyses.

Table 5.8 shows that the environmental dataset can be reduced to nine variables that exert a statistically significant independent influence on diatom distributions. When Alk, EC, TP, Na, K, Cl, Mg, Chla and SD, are entered into a CCA with the 83 diatom taxa, both CCA axis 1 ($P = 0.001$) and all canonical axes ($P = 0.001$) are significant. The results of a CCA including these nine remaining environmental variables are presented in Table 5.9. The removal of a further eight environmental variables decreases the total explained variance to approximately 75% of that portrayed by 17 variables, and 50% of that described by all 26 environmental variables (Tables 5.4, 5.6 and 5.9), indicating that the remaining variables are still capable of explaining a large proportion of the species variation.

Variable	Partially constrained CCA			
	λ_1	λ_2	λ_1/λ_2	p value
Alk				sole var.[1]
EC	0.166	0.442	0.376	0.006[1]
Na	0.148	0.453	0.327	0.013[1]
Cl	0.147	0.449	0.327	0.017[1]
K	0.143	0.463	0.309	0.019[1]
TP	0.141	0.461	0.306	0.025[1]
TON	0.124	0.439	0.282	0.063[1]
Type	0.116	0.444	0.261	0.104[1]
SRP	0.110	0.480	0.229	0.146[1]
Ca	0.081	0.456	0.178	0.499[1]
Geol	0.071	0.485	0.146	0.688[1]
Mg				sole var.[2]
pH	0.095	0.476	0.200	0.287[2]
Chla				sole var.[3]
SD	0.196	0.388	0.505	0.001[3]
Age	0.107	0.448	0.239	0.168[3]
ChlaM	0.096	0.469	0.205	0.323[3]

Table 5.8 **Results of pCCA analyses. The number in superscript adjacent to the p-values indicates each variable's group membership for pCCAs. Variables are ranked within each group according to statistically significant independent influence on diatom species distributions.**

Axis	Eigenvalue	Species / environment correlation	Cumulative % variance (species)	Cumulative % variance (species / environment)	Sum of all unconstrained eigenvalues	Sum of all canonical eigenvalues
1	0.330	0.912	9.1	26.2		
2	0.248	0.803	15.9 (6.8)	46.0 (19.8)		
3	0.202	0.776	21.5 (5.6)	62.1 (16.1)		
4	0.150	0.806	25.6 (4.1)	74.0 (11.9)		
					3.630	1.256

Table 5.9 Results of CCA on the 83 diatom species with 42 active sites and 9 environmental variables (numbers in parentheses are individual axis contributions).

5.4.8 Examination of Variance Inflation Factors (VIFs)

Following reduction of the data-set to nine environmental variables, which all exerted an independent influence on diatom species distributions, a further CCA was run to identify variables which had VIFs >20. The VIF is used by ter Braak & Šmilauer (1998) to assess the independent contribution of each environmental variable to the overall ordination. If variables have VIFs >20, it is argued that they should be removed from the analysis in turn (largest removed first), until all VIFs <20. However, some authors remove variables until all VIFs are <10 (Philibert & Prairie, 2002a). In this study, the latter approach was adopted to further minimise inter-correlation between the remaining environmental variables.

EC had the highest VIF (25). This was probably due to its high correlation with the individual measured cations and anions (Na^+, K^+, Mg^{2+}, Ca^{2+} and Cl^-), whose proportional concentrations contribute to the overall conductance of the water. EC was subsequently removed from the suite of explanatory environmental variables and the analysis re-run with eight variables. Following EC's removal, Na still exhibited a high VIF of 14. Since Na is strongly positively correlated with the remaining cations and anions in the data-set (Pearson's correlation coefficients of Na:Cl = 0.95, Na:K = 0.84 and Na:Mg = 0.40 (Table 4.5)), it was decided that removal of Na^+ was warranted. Consequently, Na was removed and the analysis re-run with the remaining seven variables. Following sequential removal of EC and Na from the CCA, all VIF scores were <3, indicating minimal covariation between the remaining seven variables. Tables 5.10 and 5.11 illustrate the results of the above CCAs. Figures 5.6a and 5.6b display the ordination triplots of axis 1 vs. axis 2, and axis 1 vs. axis 3 for the latter CCA – the triplot relating to the former CCA is not displayed because of its close similarity to the latter.

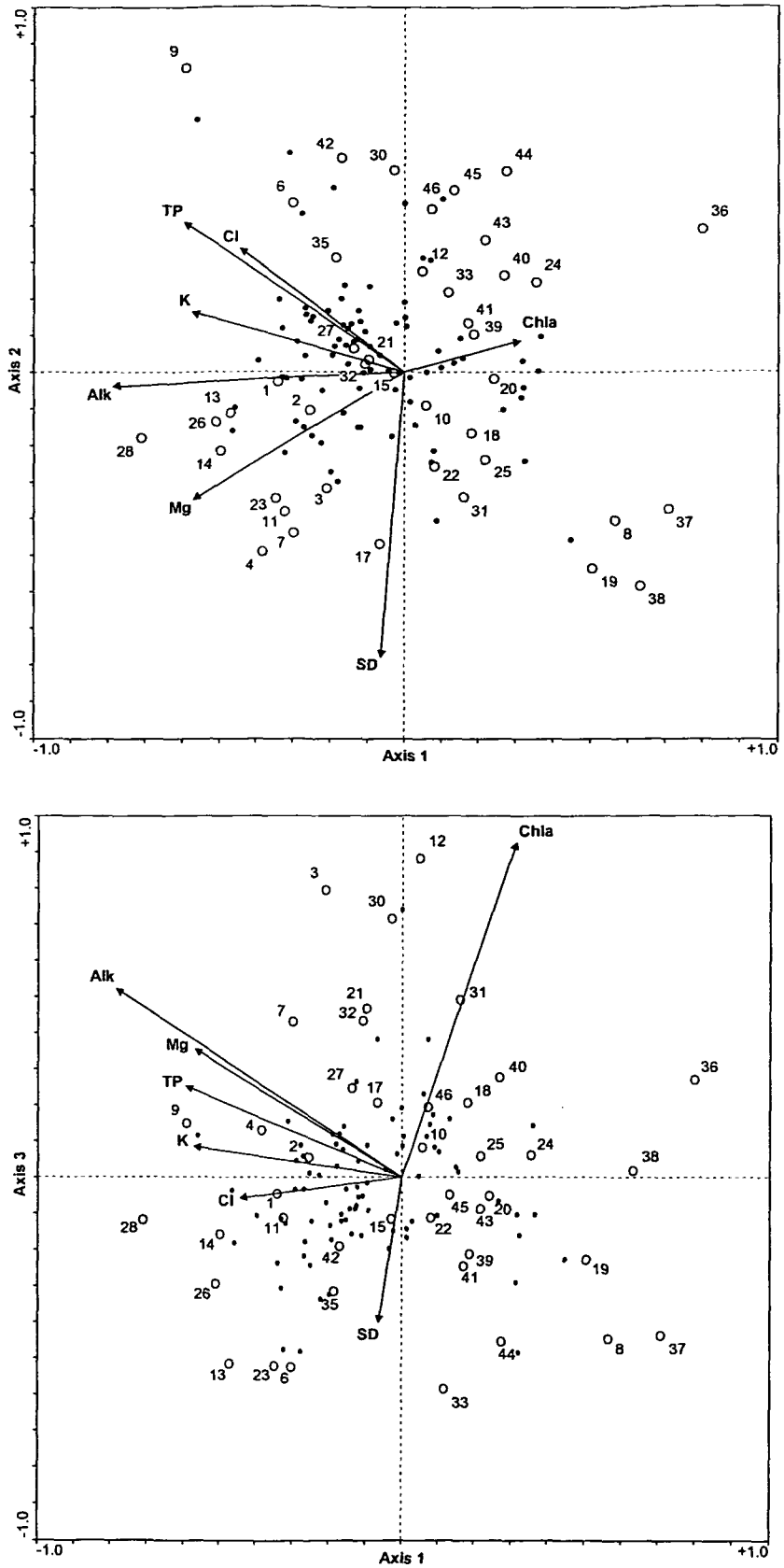


Figure 5.6a/b CCA tri-plots illustrating 7 environmental vectors and 83 diatom species from 42 sites (a) axes 1 and 2; b) axes 1 and 3). Environmental vectors are labelled, sites are numbered, but species (black circles) are not named for clarity.

Axis	Eigenvalue	Species / environment correlation	Cumulative %.variance (species)	Cumulative % variance (species / environment)	Sum of all unconstrained eigenvalues	Sum of all canonical eigenvalues
1	0.315	0.903	8.7	26.8		
2	0.241	0.793	15.3 (6.6)	47.2 (20.4)		
3	0.199	0.765	20.8 (5.5)	64.1 (16.9)		
4	0.149	0.800	24.9 (4.1)	76.8 (12.7)		
					3.630	1.179

Table 5.10 Results of CCA on the 83 diatom species with 42 active sites and 8 environmental variables (numbers in parentheses are individual axis contributions).

The removal of EC from the environmental variable dataset reduces the eigenvalue of axis 1 (0.330 to 0.315) and decreases the percentage variance in the species data explained by this axis (9.1% to 8.7%). This was expected, since EC had a strong relationship with axis 1 and explained considerable variation in the species data as shown by partial CCA (Table 5.8). However, the total explained variance is only reduced from 34.6% to 32.5% (Tables 5.9 and 5.10); indicating that EC's high intercorrelation with other variables in the dataset does not greatly reduce the explanatory power of the analysis and supports the redundancy of this variable. Furthermore, removal of Na from the dataset has minimal influence on the results of CCA, providing support for its redundancy as an explanatory variable (Tables 5.10 and 5.11).

Axis	Eigenvalue	Species / environment correlation	Cumulative % variance (species)	Cumulative % variance (species / environment)	Sum of all unconstrained eigenvalues	Sum of all canonical eigenvalues
1	0.314	0.904	8.6	28.1		
2	0.237	0.792	15.2 (6.6)	49.4 (21.3)		
3	0.199	0.763	20.7 (5.5)	67.2 (17.8)		
4	0.148	0.795	24.7 (4.0)	80.5 (13.3)		
					3.630	1.116

Table 5.11 Results of CCA on the 83 diatom species with 42 active sites and 7 environmental variables (numbers in parentheses are individual axis contributions).

5.4.9 Forward selection of environmental variables

Manual forward selection was applied to the seven remaining environmental variables to identify a sub-set of those variables that could statistically explain the variance in the species data almost as well as the full environmental variable data-set. Forward selection ranks the environmental variables according to the variance they explain in the diatom species data.

Variable	Order added	Before (marginal effects)	Added (conditional effects)	p-value	% total variance explained
Alk	1	0.259	0.259	0.001	23.2
Chla	2	0.207	0.221	0.001	19.8
TP	3	0.200	0.140	0.025	12.5
Mg		0.199			
SD	4	0.196	0.159	0.006	14.2
K	5	0.184	0.126	0.025	11.3
Cl		0.164			
Total		1.409	0.905 (of 1.116)		81.0

Table 5.12 Results of manual forward selection of environmental variables for the final CCA. P-values are generated from Monte Carlo permutation tests with 999 unrestricted permutations.

The forward selection results presented in Table 5.12 show that five of the measured environmental variables make independent and significant contributions to explaining the variance in the species data. The most significant of these is Alk, which explains 23.2% of the total variance explained by all the measured environmental variables. Chla, TP, SD and K explain a further 14.0%, 8.7%, 9.9% and 7.8% respectively, in total explaining 64.2% of the total variance in the species data. Following inclusion of Alk, Chla, TP, SD and K in the manual forward selection process, Mg and Cl failed to contribute additional statistically significant explanatory power. Further support for the elimination of Cl and Mg is derived from their extreme concentrations (>2.5 standard deviations from the mean value) in at least one site. Cl showed an extremely high concentration in Bough Beech (site 42) and the Mg concentration in Tittesworth (site 33) was particularly low. Rather than removing a further two sites from the calibration set, it was deemed more appropriate to remove two environmental variables that could be adequately represented by other intercorrelated variables (i.e. K and Alk). The remaining 5 variables all loaded significantly on either one or both CCA axes 1 and 2. The results of a final CCA constrained to these five variables alone are presented in Table 5.13 and Figure 5.7.

Axis	Eigenvalue	Species / environment correlation	Cumulative % variance (species)	Cumulative % variance (species / environment)	Sum of all unconstrained eigenvalues	Sum of all canonical eigenvalues
1	0.306	0.884	8.4	33.8		
2	0.202	0.796	14.0 (5.6)	56.2 (22.4)		
3	0.188	0.697	19.2 (5.2)	76.9 (20.7)		
4	0.120	0.755	22.5 (3.3)	90.2 (13.3)		
					3.630	0.905

Table 5.13 Results of CCA on the 83 diatom species with 42 active sites and 5 environmental variables (numbers in parentheses are individual axes contributions).

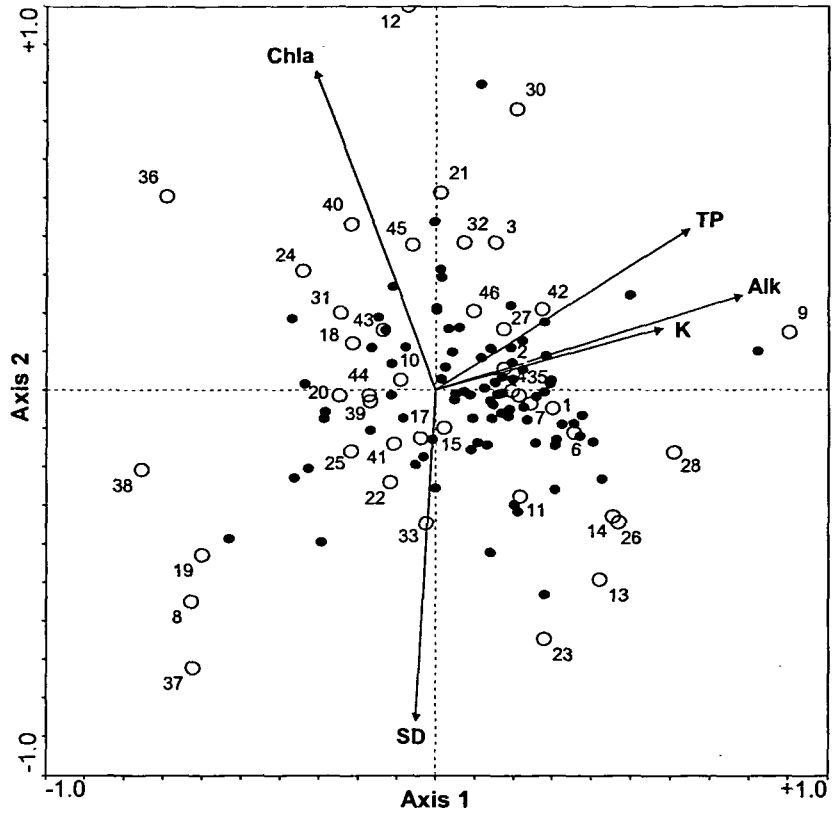


Figure 5.7 **CCA tri-plot illustrating 5 environmental variable vectors and 83 diatom species from 42 sites (axes 1 and 2). Environmental vectors are labelled, sites are numbered, but species (black circles) are not named for clarity.**

The first two axes in the final CCA analysis of the 42-reservoir dataset boast respective eigenvalues of 0.306 and 0.203 and explain 8.4% and 5.6% of the variance in the diatom species data. The first four axes account for approximately a quarter of the total diatom species variance (37% of that explained by all 26 variables), indicating the importance of the five forward-selected variables in explaining variance in diatom species distributions across the dataset. The first two axes collectively explain a relatively high percentage (56.2%) of the variance in the species-environment relationship, and the species-environment relationship is highly correlated with both CCA axis 1 (0.884) and 2 (0.796). The axis 1 and axis 2 eigenvalues are dissimilar between the full environmental dataset of 26 variables and the reduced dataset of only 5 variables. This indicates that correlation between environmental variables caused over-inflation of the axes in the initial CCA, and the removal of redundant variables was necessary and justified. Figure 5.7 shows that when the five forward-selected environmental variables are plotted in a CCA ordination diagram, Alk, TP and K are all highly positively correlated with axis 1, whilst Chla and SD are strongly related to axis 2 but in approximately equal and opposite directions. Whilst it has

been shown that the five remaining variables all explain statistically significant independent variation in the diatom species assemblages, there are essentially two main axes of variation in the dataset, one related to water chemistry and the other to biological productivity.

5.4.10 Variance Partitioning

Variance partitioning (Borcard *et al.* 1992) employs canonical ordination (i.e. CCA), and is used in this study to examine correlations between diatom assemblages and environmental variables. The percentage of the total variance in diatom assemblages explained by i) individual environmental variables independent of all other measured variables, and ii) the combined effects of two or more factors are assessed. This enables an evaluation of the strength and significance of the unique contribution of individual factors influencing diatom assemblages, in addition to an assessment of the degree of interaction between factors.

Canonical correspondence analysis of the 42-reservoir dataset indicates that measured variables explain approximately 25% of the variance in the diatom data (sum of canonical eigenvalues as a proportion of all unconstrained eigenvalues - Table 5.13). A CCA run with TP as the sole environmental variable showed that TP could explain 5.51% of the variance in the species data. However, a CCA run with TP as the only environmental variable and the other four environmental variables as covariables showed an overlap of 3.42% leaving a discrete contribution of only 2.09%. Alk explained 7.14% and made a discrete contribution of 4.38%. K explained 5.06% and made a discrete contribution of 2.42%. SD explained 5.54% and made a discrete contribution of 5.07%. Chla explained 5.73% and made a discrete contribution of 5.70%.

The above variance partitioning exercise indicates that Chla explains the greatest amount of independent variation in the diatom data (Figure 5.8). Chla co-varies only with SD, although the overlap between these variables is slight (0.03%). SD co-varies with Chla (0.03%), K (0.08%) and TP (0.36%). In common with Chla, the overlap between SD and its covariables is very low. This result was to be expected, since SD and Chla demonstrated a strong relationship with the secondary CCA axes, 2 and 3 respectively, and exhibited non-significant correlations with most other environmental variables. Indeed the only highly significant relationships were with variables excluded because of their failure to explain a significant amount of variance in the diatom data during constrained ordination.

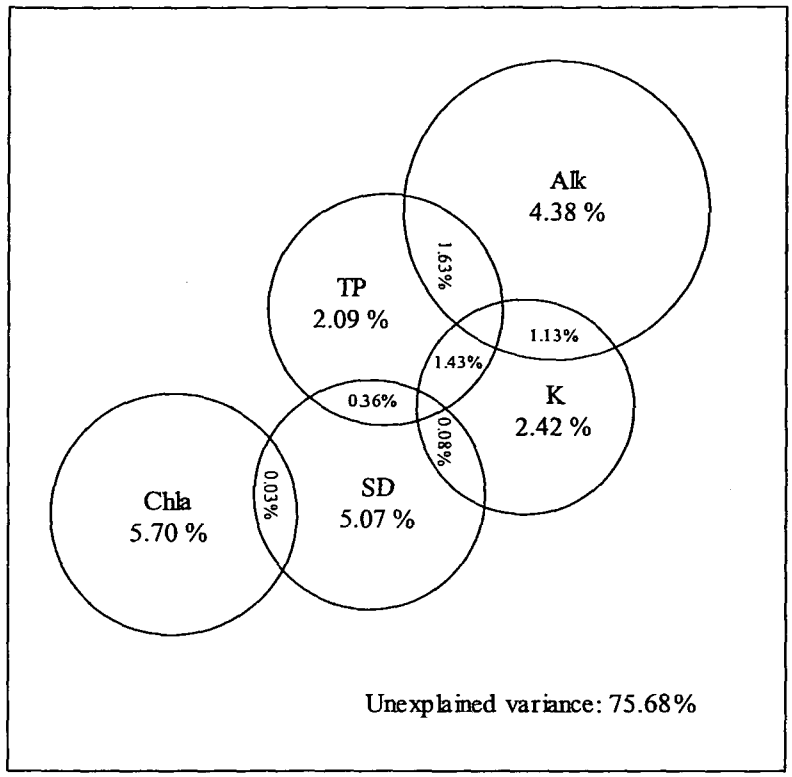


Figure 5.8 **Variance partitioning of the 42-reservoir dataset. Diatom species variance is partitioned into that which is independently explained by the five forward selected measured environmental variables (non-overlapping portions of circles), that which co-varies between variables (overlap) and that which is unexplained by the measured variables (the remainder). Circles are proportional to total variance explained (unexplained variance and overlap between circles not proportional).**

In contrast, TP, Alk and K show significant inter-correlation, despite each variable explaining significant independent variation in the species data. 62% of TP's explanatory power is derived from it co-variation with Alk, K and SD, 52% of K's influence on species variation is derived from its co-variation with Alk, TP and SD, and 39% of Alk's explanatory power originates from its relationship with TP and K. Despite the highest overall variance being explained by Alk (7.14%), the interaction it shares with the other measured variables (2.76%) reduces the proportion of independent variance that it can explain to only 4.38%.

These results may indicate that Chla and SD are the most appropriate environmental variables to exploit in the construction of inference models. TP, Alk and K may be less useful due to high inter-correlations and low discrete influences, although the results of partial CCA established that all the above variables are capable of exerting a statistically significant independent influence on diatom species distributions. However, these inferences are based only on data for the five variables included in the variance partitioning

exercise and therefore further inter-correlations (e.g. between Alk and EC) may affect the discrete variance explained by each individual variable.

5.5 Planktonic diatoms in the surface sediment dataset

Planktonic / tychoplanktonic, subsequently referred to collectively as 'planktonic', diatom species are dominant in the surface sediments of the calibration set reservoirs and it is envisaged that inference models based on 'planktonic' species alone could feasibly be created. This approach stems from the work of Siver (1999) who developed inference models based on planktonic diatoms alone, and Bradshaw *et al.* (2002) who compared the results of models developed from both full and planktonic datasets. To investigate the potential of this idea, the dataset was reduced to surface sediment 'planktonic' taxa only, and as in section 5.2 patterns of variation in the species-only and species-environment datasets were explored using DCA and CCA respectively.

In classifying habitat preferences in this study, planktonic diatoms are defined as those that spend the majority of their lifecycle in the water column or spending part of their lifecycle in the plankton and part living in other habitats (e.g. the sediment), or those growing attached to planktonic algae such as cyanophytes. Diatom habitat preferences were classified using published information (Hustedt, 1959; Canter-Lund & Lund, 1995; Cox, 1996; Krammer & Lange-Bertalot, 1986, 1988, 1991a,b) and based on modern sampling (Chapters 3 and 6).

5.5.1 General observations on surface sediment planktonic diatom species

The percentage of the flora consisting of planktonic taxa ranged from 10.0% (Cheddar) to 97.3% (Blagdon) with an overall mean of 78.0%. All but four of the reservoirs had more than 50% planktonic species and the majority of sites (33) had more than 75% (Table 5.14). The percentage of planktonic taxa in the calibration set is comparable to figures quoted in studies by Siver (1999) and Bradshaw (2001), which had means of 74% (range 20-99%) and 77% (range 5-99%) respectively.

Table 5.15 displays the names, authorities and summary abundance statistics for the 39 dominant planktonic taxa in the surface sediments of the 46-reservoir dataset. The number of planktonic diatoms (39) used for subsequent analyses is comparable to the number exploited by other researchers in the construction of inference models based solely upon surface sediment planktonic diatoms. In comparison with the current study, Siver (1999) applied slightly stricter criteria for the inclusion of taxa (see Chapter 3). Of the 40 taxa he

deemed planktonic, only 31 met his criteria. If his criteria had been employed in this study, only 36 of the 39 taxa in Table 5.15 would have been carried forward. Bradshaw (2001) included 41 species in her planktonic dataset. Evidently, the number of planktonic species incorporated will depend to some extent upon the species deemed 'planktonic' by individual researchers, as well as the degree to which some taxa are separated into their different sub-species, varieties and forms.

Table 5.15 illustrates that across the dataset the most commonly occurring planktonic diatom taxa are *A. formosa* (40 sites), *S. parvus* (37 sites), *C. radiosa* (32 sites), *Cyclostephanos invisitatus* (29 sites), *Cyclotella pseudostelligera* (28 sites), *F. crotonensis* (26 sites), *S.* cf. *agassizensis* (26 sites), *C. dubius* (25 sites), *A. granulata* (23 sites), *S. neoastraea* (23 sites), *Stephanodiscus hantzschii* (23 sites), *Melosira varians* (22 sites), *Nitzschia palea* (22 sites) and *A. ambigua* (21 sites). The taxa that occur at the greatest mean percentage relative abundances (in the sites where they occur) are *F. crotonensis* (20.9%), *A. subarctica* (17.4%), *A. subarctica* fo. *subborealis* (12.8%), *A. formosa* (15.8%), *A. islandica* (11.8%), *A. ambigua* (10.7%), *C. dubius* (9.7%) and *A. granulata* (8.6%).

5.5.2 Selection of sites for inclusion in the planktonic dataset.

Based upon their low relative abundance (<50%) of planktonic diatom taxa (Table 5.14), four sites (Cheddar (site 5); Costessey (site 9); Pitsford (site 23) and Trenchford (site 34)) were deemed inappropriate for inclusion in the planktonic diatom calibration set and were thus removed before carrying out DCA analyses.

Cheddar's water is sourced from springs and is particularly clear, with the photic zone extending to the bottom of the reservoir. It was noted in the summer of both 1999 and 2000 that dense growths of the macrophyte, *Ceratophyllum demersum* were present across the entire reservoir, thus explaining the high percentage relative abundance of epiphytic taxa such as *G. minutum*, *C. placentula* and *A. minutissima* in the surface sediment sample from this site. Pitsford's high water clarity also enables the growth of high percentage infestations of macrophytes in particular *Elodea* spp., *Chara vulgaris*, *Zannichellia palustris*, explaining the high percentage abundance of the epiphytes, *C. placentula*, *R. abbreviata* and *A. minutissima* at this site. Costessey is a shallow site that supports growths of both macrophytes and macroalgae (*Cladophora* spp.), again explaining the presence of numerous periphytic taxa in the surface sediments of this site. Trenchford has the lowest pH of all reservoirs sampled in this study and has high water clarity that enables the growth of benthic diatoms on the sediment surface e.g. *F. brevistriata*.

Site	% relative abundance of planktonic species	Dominant species (including both planktonic and periphytic species)
1	74.2	*AulGr* (25%); *ActNormS* (18%); *StNeo* (7%); *StCfAgas* (7%)
2	94.3	*AstForm* (39%); *StNeo* (10%); *ActNormS* (10%); *AulIslan* (6%)
3	97.3	*FraCrot* (64%); *AulGr* (20%); *CycsInv* (8%)
4	82.2	*AulGr* (37%); *ActNormS* (13%); *StNeo* (10%); *AstForm* (7%); *FraCrot* (6%)
5	10.0	*GomMint* (33%); *CocPlac* (13%); *AchMin* (10%)
6	56.3	*AulAmb* (18%); *StCfAgas* (16%)
7	79.7	*FraCrot* (62%); *AulGr* (13%)
8	94.5	*AstForm* (22%); *AulAmb* (20%); *AulSub* (16%)
9	46.1	*StHantzT* (27%); *CycsInv* (10%); *CocPlac* (10%)
10	95.0	*FraCrot* (72%); *AulGran* (7%); *AulIslan* (6%)
11	96.9	*AstForm* (57%); *CycsDub* (16%); *StNeo* (15%)
12	90.6	*AulSubB* (19%); *CycsDub* (17%); *StParvus* (14%); *StCfAgas* (11%); *CycAtm* (7%)
13	72.2	*AstForm* (59%); *CycRad* (4%)
14	75.9	*AstForm* (19%); *CycPseu* (18%); *CycsDub* (8%); *CycMeng* (6%); *StNeo* (5%)
15	62.3	*AstForm* (44%); *CycRad* (6%); *AchMin* (6%); *CycPseu* (5%)
16	75.8	*StNeo* (32%); *AulGrA* (27%); *AstForm* (7%); *StCfAgas* (6%)
17	77.8	*FraCrot* (25%); *CycRad* (21%); *AstForm* (12%);
18	94.9	*AulAmb* (38%); *FraCrot* (32%); *AulGrA* (7%); *CycsDub* (5%)
19	55.7	*FraConC* (31%); *FraCrot* (23%); *AulSub* (18%); *AstForm* (7%)
20	80.7	*FraCrot* (33%); *AulSub* (17%); *FraBrev* (12%); *CycRad* (8%)
21	(58.5) 92.1	***CycCom* (29%)**; *CycRad* (18%); *CycsDub* (12%); *AulIslan* (4%); ***CycKram* (4%)**
22	84.1	*FraCrot* (21%); *AstForm* (17%); *CycPseu* (14%); *AulAmb* (10%); *StAlp* (8%)
23	38.1	*AstForm* (29%); *CocPlac* (11%); *RhAbbrev* (9%); *AchMin* (6%); *FraVau* (6%)
24	94.7	*AulSub* (60%); *CycsDub* (13%); *AulGr* (12%)
25	77.5	*FraCrot* (60%); *AstForm* (12%)
26	67.1	*CycsInv* (25%); *CycAtm* (11%); *StNeo* (11%)
27	77.1	*AulGrA* (27%); *StParvus* (22%); *CycsInv* (8%); *CycRad* (6%)
28	74.8	*ActNormS* (29%); *StCfAgas* (13%); *AulGrA* (8%); *StAlp* (5%); *CycAtm* (5%)
29	64.7	*TabFloc* (41%); *CycRad* (11%); *FraVau* (8%); *AstForm* (7%)
30	91.8	*AulSubB* (43%); *StCfAg* (24%); *StParvus* (10%); *CycRad* (7%)
31	80.6	*AulIslan* (31%); *StParvus* (28%); *AulGr* (13%); *FraCrot* (4%)
32	83.1	*AulGr* (42%); *FraCrot* (17%); *StParvus* (8%)
33	87.7	*AstForm* (36%); *AulSub* (15%); *TabFloc* (11%); *StParvus* (8%); *CycRad* (6%)
34	(27.6) 39.3	*FraBrev* (35%); *Cyc Rad* (19%); ***AulAlpg* (6%)**; *TabFloc* (5%); ***SynTen* (5%)**
35	62.3	*NitzFont* (8%); *CycMeng* (8%); *CycPseu* (7%); *AulSub* (7%); *CycsDub* (7%)
36	94.1	*AulSub* (30%); *AulAmb* (21%); *CycsDub* (12%); *AstForm* (9%); *StParvus* (8%)
37	92.3	*AulAmb* (37%); *AstForm* (25%); *AulSub* (21%); *CycRad* (4%)
38	91.7	*AstForm* (27%); *FraCrot* (26%); *AulSub* (19%); *StParvus* (13%)
39	87.4	*FraCrot* (45%); *StParvus* (8%); *AulGr* (7%); *AstForm* (5%); *AulAmb* (5%)
40	83.7	*AulSub* (36%); *AulAmb* (14%); *StParvus* (12%); *CycRad* (8%)
41	86.5	*AulSub* (40%); *FraCrot* (29%); *StParvus* (6%); *CycRad* (5%)
42	82.9	*CycsDub* (40%); *StCfAgas* (9%); *ThalBram* (9%); *CycsInv* (6%)
43	83.7	*AulAmb* (44%); *CycsDub* (18%); *StParvus* (5%)
44	89.5	*AulSub* (36%); *CycsDub* (32%); *StParvus* (7%); *StCfAgas* (6%); *CycsInv* (4%)
45	80.7	*CycsDub* (23%); *CycRad* (20%); *StHantzT* (7%); *CycPseu* (6%); *AstForm* (5%)
46	89.0	*CycsDub* (20%); *CycRad* (16%); *StHantz* (11%); *AulGrA* (9%); *AstForm* (6%)
	Mean = 78.0	

Table 5.14 **The percentage relative abundance of planktonic diatom taxa in the surface sediments of 46 reservoirs, and the dominant species (both planktonic and periphytic) contributing to these data. Sites with < 50% planktonic diatoms in their surface sediments are highlighted. Planktonic species in sites 21 and 34 which failed to meet criteria for inclusion in the surface sediment planktonic diatom calibration set are written in bold and the percentage relative abundance of planktonic diatom taxa in these sites both before and after (bracketed figures) exclusion of these species are presented. For species abbreviations please see Appendix 3.**

Taxon	*n*	Mean	Min	Max	SD
Actinocyclus normanii fo. *subsalsa* (Juhl.-Dannf.) Hust. ex VanLand.,1967	11	6.7	0.2	28.6	9.5
Asterionella formosa Hassall 1850	40	12.1	0.3	59.4	15.8
Aulacoseira ambigua (Grun. in Van Heurck) Simonsen 1979	21	10.7	0.2	44.2	13.9
Aulacoseira granulata (Ehrenb.) Simonsen 1979	23	8.6	0.4	42.2	12.0
Aulacoseira granulata var. *angustissima* (O.Müll.) Simonsen 1979	19	5.6	0.2	27.2	8.0
Aulacoseira granulata var. *angustissima* fo. *curvata*	2	2.6	2.6	2.7	0.1
Aulacoseira islandica (O.Müll) Simonsen 1979	4	11.8	4.4	31.0	12.8
Aulacoseira subarctica (O.Müll) Haworth	19	17.4	0.2	59.5	16.4
Aulacoseira subarctica fo. *subborealis* (O.Müll) Haworth	5	12.8	0.2	42.9	18.6
Cyclostephanos dubius (Fricke in A.Schmidt) Round 1982	25	9.7	0.2	40.1	10.7
Cyclostephanos invisitatus Theriot, Stoermer & Håkannson comb. Nov. 1987	29	2.9	0.1	24.7	4.8
Cyclostephanos cf. *tholiformis* Stoermer, Håkannson & Theriot 1987	16	1.7	0.2	7.9	2.1
Cyclotella atomus Hust. 1937	14	2.4	0.2	10.7	3.1
Cyclotella meneghiniana Kütz. 1844	20	1.6	0.2	7.8	2.2
Cyclotella ocellata Pant. 1902	3	1.6	0.1	2.7	1.4
Cyclotella pseudostelligera Hust. 1939	28	3.1	0.2	18.0	4.2
Cyclotella radiosa (Grun.) Lemmermann & Håkannson 1988	32	6.2	0.2	21.2	6.3
Diatoma tenuis var. *elongatum* Lyngb. 1819	11	0.5	0.1	1.7	0.5
Diatoma vulgaris Bory 1824	13	1.4	0.2	2.8	1.1
Fragilaria capucina var. *mesolypta* (Rabenh.) Rabenh. 1864	17	1.0	0.2	3.0	0.9
Fragilaria crotonensis Kitton 1869	26	20.9	0.2	72.4	23.0
Melosira varians Ag. 1827	22	1.1	0.1	3.4	1.1
Nitzschia fonticola Grunow	20	1.0	0.2	8.4	1.8
Nitzschia gracilis Hantzsch. 1860	8	0.8	0.3	1.3	0.3
Nitzschia palea (Kütz.) W.Sm. 1853	22	0.8	0.2	1.9	0.6
Stephanodiscus cf. *agassizensis* Håkansson & Kling sp.nov. 1989	26	5.2	0.2	24.0	5.7
Stephanodiscus alpinus Hustedt in Huber-Pestalozzi	6	3.2	0.4	7.8	2.9
Stephanodiscus hantzschii Grun. in Cleve & Grun. 1880	23	1.2	0.2	10.8	2.2
Stephanodiscus hantzschii fo. *tenuis* (Hust.) Håkannson & Stoermer stat nov. 1984	15	2.8	0.2	24.3	6.2
Stephanodiscus neoastraea Håkannson & Hickel 1986	23	5.0	0.2	31.9	7.0
Stephanodiscus parvus Stoermer & Håkannson 1984	37	5.4	0.4	27.5	6.1
Synedra acus var. *angustissima* (Grun. in Van Heurck) Van Heurck 1885	4	0.6	0.3	1.4	0.5
Synedra acus var. *radians* (Kütz.) Hust. 1930	12	0.6	0.2	1.7	0.5
Synedra rumpens Kütz. 1844	12	0.8	0.2	3.1	0.8
Synedra rumpens var. *familiaris* (Kütz.) Hust. 1930	3	2.0	1.0	3.3	1.2
Synedra rumpens var. *fragilarioides* Grun. in Van Heurck 1881	4	0.7	0.2	1.9	0.8
Synedra rumpens var. *scotica* Grun. in Van Heurck 1881	2	1.7	0.4	3.0	1.8
Tabellaria flocculosa (Roth) Kütz. 1844	8	8.2	0.2	40.6	13.7
Thalassiosira bramaputrae (Ehrenb.) Håkannson & Locker 1981	2	4.9	1.3	8.6	5.2

Table 5.15 Diatom species classified as planktonic in this study, that occur in at least two sites and at ≥1% relative abundance in at least one site. The number of sites in which each species occurs, and their mean, minimum and maximum abundances and standard deviations are displayed. (Data for 46 sites and 39 species)

Both Cheddar and Trenchford were made passive in DCA analyses of the full diatom training due to their outlier status in terms of diatom habitat / life-form. This further supports their removal from a planktonic calibration set, where dominance by species typically found in periphytic habitats is undesirable. This results in a 'planktonic' dataset consisting of 42 sites and 39 species – removal of sites 5, 9, 23 and 34 did not affect the number of species meeting the criteria for inclusion.

5.6 Detrended Correspondence Analysis (DCA): Planktonic diatoms

As with the full species dataset, DCA was employed to investigate the planktonic dataset. The results in Table 5.16 show that the first two DCA axes (λ_1 = 0.532; λ_2 = 0.429) accounted for 23.1% of the variation in the diatom species data (Axis 1 = 12.8% and axis 2 = 10.3%), and included species gradients with lengths of 3.110 and 3.896 standard deviation units respectively.

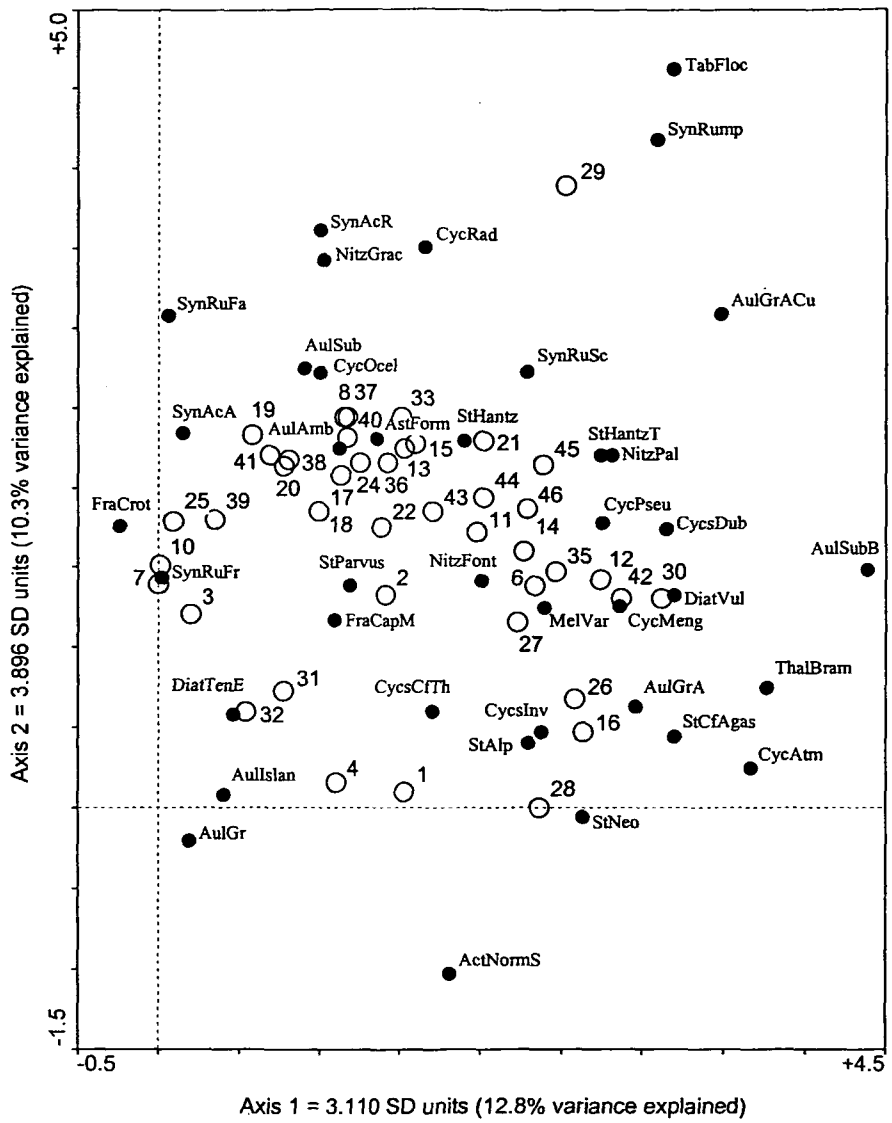


Figure 5.9 DCA biplot illustrating 39 planktonic diatom species (black circles) in 42 sites (open circles).

It is clear from the DCA ordination biplot illustrated in Figure 5.9 that site 29 (Stithians) is an outlier in terms of its diatom species assemblage, and its presence in the ordination increases the amount of variation in the species data explained by axis 2. Since site 29 appears to exert considerable influence on the length of axis 2, confining the remaining data

to a smaller area of the ordination space, its removal from subsequent analysis is considered justified.

Axis	Eigenvalue	Length of gradient (SD units)	Cumulative variance represented (%)
1	0.532	3.110	12.8
2	0.429	3.896	23.1 (10.3)
3	0.276	2.652	29.7 (6.6)
4	0.190	2.907	34.3 (4.6)

Table 5.16 Results of DCA on the 39 planktonic species with 42 active sites (numbers in parentheses are individual axes contributions).

5.6.1 DCA: Removal of outliers

The results of a DCA with 41 active sites, and site 29 made passive, are presented in Table 5.17. This illustrates that the amount of variation in the species data explained by axis 2 decreases (12.8% to 9.8%) and the gradient length of axis 2 is reduced from 3.896 (Table 5.16) to 2.474 standard deviation units. The axis 1 eigenvalue and gradient length does not change significantly, indicating that the removal of site 29 barely affects the main axis of variation in the species data. However, removal of this outlier allows the overall variation in the site and species data to be more clearly expressed.

Axis	Eigenvalue	Length of gradient (SD units)	Cumulative variance represented (%)
1	0.530	3.158	13.8
2	0.379	2.474	23.6 (9.8)
3	0.205	2.255	29.0 (5.4)
4	0.147	1.982	32.8 (3.8)

Table 5.17 Results of DCA on the 39 planktonic species with 41 active sites (numbers in parentheses are individual axes contributions).

Figure 5.10 displays the DCA ordination diagram illustrating 41 active sites and 39 planktonic diatom species. Overlain on this diagram are four hulls, grouping sites according to the results of TWINSPAN classification. The site groupings and associated species are very similar to those for the full dataset displayed in Figure 5.2a, which includes both periphytic and planktonic diatoms. This is perhaps to be expected because of the overall dominance of planktonic diatoms across the dataset, which are providing the driving force for both the ordination and classification. However, the inclusion of only plankton-dominated sites appears to reduce overlap between groups and thus improves their visual delineation.

The lengths of the species gradients (axis 1 = 3.2 SD units; axis 2 = 2.5 SD units) revealed by DCA analysis of the planktonic dataset indicate that most species' responses would be accurately approximated by unimodal response models (Jongman *et al.*, 1995). It is therefore appropriate that CCA is utilised for the ensuing exploration of species-environment interactions. This is in line with the outcome of DCA for the full dataset (section 5.3).

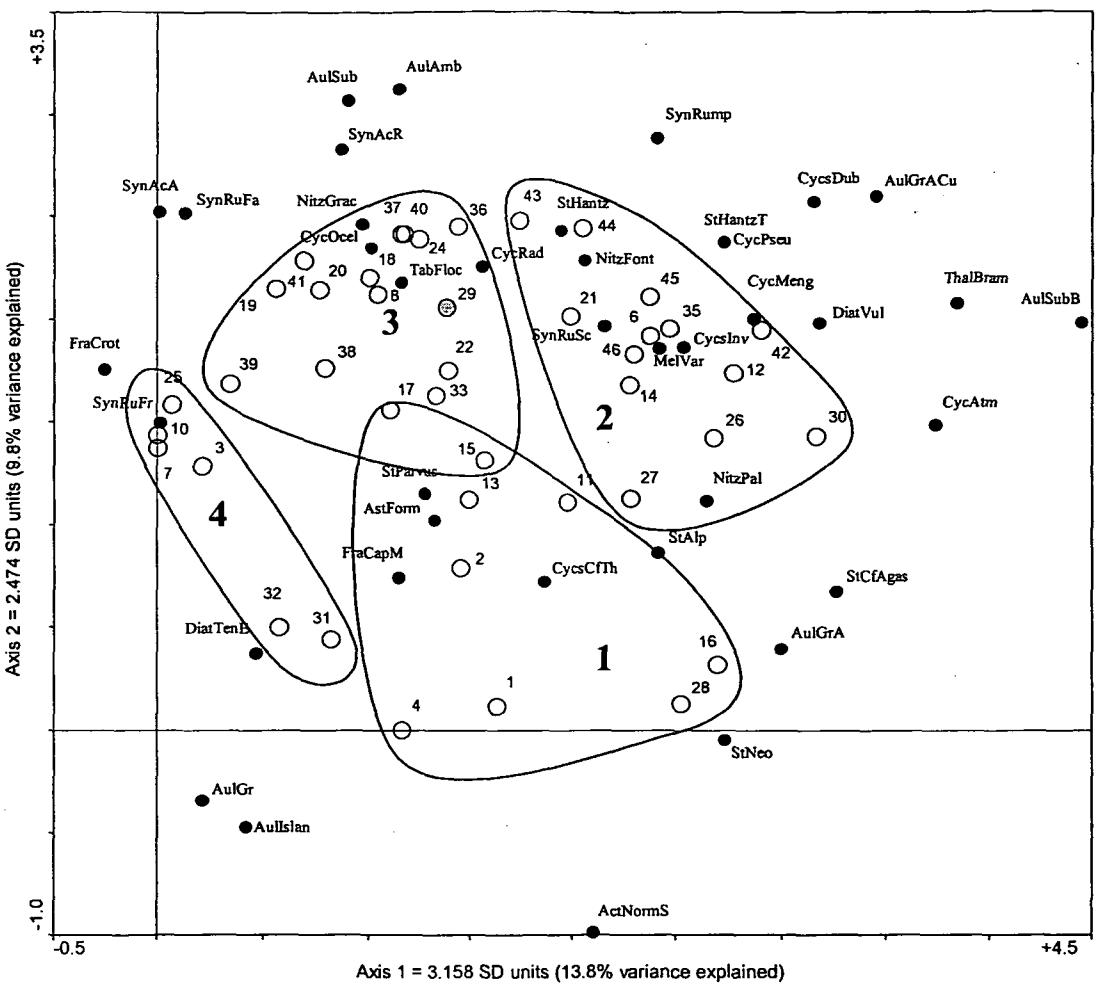


Figure 5.10 DCA biplot illustrating 39 planktonic diatom species (black circles) in 41 sites (open circles - passive site 29 is shaded). Sites are grouped according to TWINSPAN results.

5.7 Canonical Correspondence Analysis (CCA): Planktonic dataset.

5.7.1 Data screening prior to the application of CCA.

Following the application of PCA (section 4.5) and DCA (section 5.3) techniques, the surface sediment planktonic diatom dataset consists of 39 planktonic diatom species and 40 sites. During preliminary data screening, sites 5, 9, 23 and 34 were removed due to their low

relative abundance of planktonic species. Site 29 was removed because of its outlier status highlighted in DCA and site 16 was deemed an outlier and subsequently removed because of its extreme water chemistry revealed in PCA.

5.7.2 Selection of environmental variables for inclusion within CCA.

The planktonic dataset was treated in the same way as the full dataset. First, a series of constrained CCAs were performed, using each environmental variable as the sole explanatory variable. This resulted in a reduced dataset of 14 variables, all of which exerted an independent influence on species distributions (as assessed by 999 unrestricted Monte Carlo permutations).

Variable	% species variance	Constrained CCA λ_1	λ_2	λ_1/λ_2	p value	Partially constrained CCA λ_1	λ_2	λ_1/λ_2	p value
Alk	7.5	0.279	0.525	0.531	0.001				sole var.[1]
EC	7.1	0.264	0.521	0.507	0.001	0.268	0.515	0.520	0.001[2]
Mg	6.1	0.229	0.523	0.438	0.001	0.145	0.522	0.278	0.048[2]
SD	6.0	0.224	0.490	0.457	0.003	0.220	0.432	0.509	0.002[2]
K	5.5	0.206	0.513	0.402	0.004	0.208	0.507	0.410	0.003[2]
TP	5.3	0.198	0.514	0.385	0.006				sole var.[3]
Chla	5.3	0.199	0.521	0.382	0.001				sole var.[2]
Geol	5.2	0.192	0.525	0.366	0.003	0.070	0.521	0.134	0.773[1]
Na	4.9	0.183	0.507	0.361	0.008	0.182	0.502	0.363	0.006[2]
SRP	4.9	0.183	0.525	0.349	0.007	0.153	0.496	0.308	0.063[3]
Cl	4.6	0.173	0.504	0.343	0.013	0.172	0.499	0.345	0.012[2]
ChlaM	4.5	0.169	0.518	0.326	0.021	0.072	0.518	0.137	0.715[2]
PH	4.4	0.164	0.517	0.317	0.032	0.068	0.490	0.139	0.775[1]
Ca	4.4	0.164	0.518	0.317	0.029	0.168	0.514	0.327	0.018[2]

Table 5.18 Results of constrained CCA and pCCA analyses. Only variables which exerted independent significance in constrained CCAs are presented. The number in superscript adjacent to the pCCA p-value indicates each variable's group membership for pCCAs. Shaded areas show statistically significant results.

Following examination of constrained CCAs (Table 5.18), along with the Pearson's weighted correlation coefficients (Table 4.6) and inter-set correlations (Table 5.19), the 14 variables were divided into intercorrelated groups representing different axes of variation in the species data. The variable from each group best explaining both significant independent variation and representing the group's axis of variation in the species data was designated group representative. This was entered into a partial CCA as the sole covariable, with each other group member entered in turn as the sole explanatory variable. This enabled determination of variables that were intercorrelated but which also explained an independent and significant (999 Monte Carlo permutations) amount of species variation.

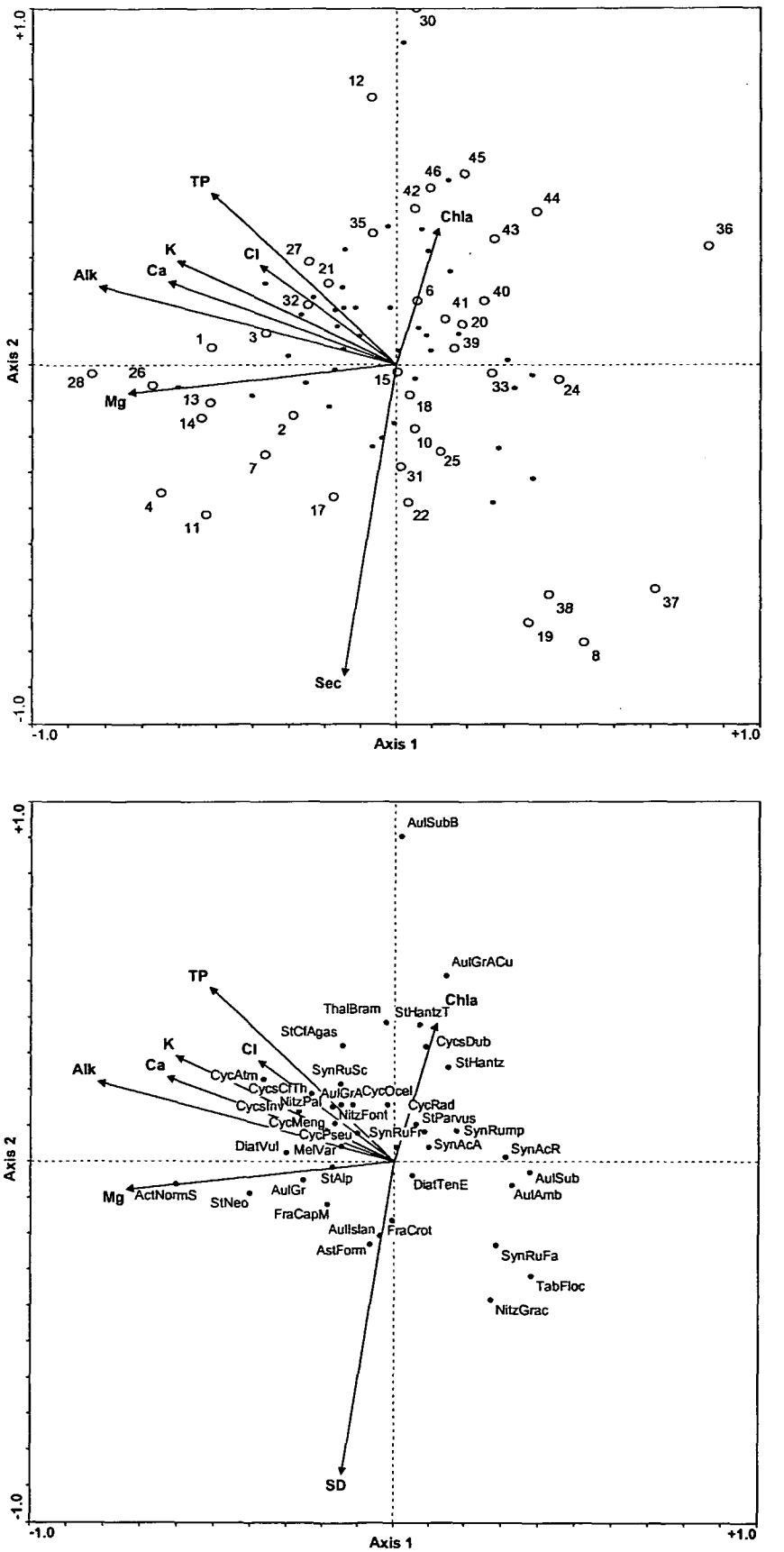
Ten environmental variables demonstrated a significant influence on species distributions. CCA axis 1 is characterised by Alk. CCA axis 2 is represented by Chla, EC, Mg, K, SD, Na, Cl and Ca, and CCA axis 3 is an expression of TP.

Variable	Inter-set correlation		
	Axis 1	Axis 2	Axis 3
pH	-0.3223	0.1324	0.0787
Mg	-0.2250	0.0352	0.1221
Alk	-0.2042	0.0962	0.0836
Geol	-0.1926	-0.1511	0.0305
Chla	0.0971	0.4968	0.3023
Na	-0.2561	-0.4210	0.2662
Cl	-0.2884	-0.3515	0.2859
ChlaM	-0.1013	0.2979	0.2162
K	-0.0646	-0.2973	0.1095
EC	-0.2299	-0.2371	0.1256
SD	0.2112	-0.2357	-0.2109
Ca	-0.0605	-0.1319	-0.0065
TP	-0.0702	-0.1011	0.4680
SRP	0.1141	0.0128	0.1671

Table 5.19 **Inter-set correlations between the 14 measured environmental variables selected in constrained CCAs and the first three CCA axes. Shaded boxes indicate the axis to which each variable is most highly correlated.**

5.7.3 Removal of inter-correlating variables by examination of VIFs

A CCA was run using the ten remaining variables. This indicated that EC should be eliminated due to its high VIF of 26. With EC removed and a CCA run using nine variables, the amount of variation in the species data that could be explained by axis 1 decreased from 8.9% (Table 5.20) to 8.7% (Table 5.21). Further examination of VIFs indicated that Na should also be removed because it had a VIF of 13 and was almost perfectly correlated with Cl (Pearson's correlation coefficient Na:Cl of 0.94). Following removal of EC and Na in turn, the eight remaining variables all showed low VIFs of between 2 and 4, indicating the satisfactory elimination of multicollinearity from the environmental dataset. The results of a CCA run with the eight remaining environmental variables, 39 planktonic species and 40 sites are presented in Table 5.22 and Figure 5.11.



Figures 5.11 a & b CCA tri-plots illustrating eight environmental vectors and a) 40 sites, b) 39 planktonic diatom species.

Axis	Eigenvalue	Species / environment correlation	Cumulative % variance (species)	Cumulative % variance (species / environment)	Sum of all unconstrained eigenvalues	Sum of all canonical eigenvalues
1	0.332	0.895	8.9	24.4		
2	0.288	0.791	16.6 (7.6)	45.5 (21.6)		
3	0.237	0.795	23.0 (6.2)	62.9 (17.4)		
4	0.162	0.752	27.3 (4.3)	74.8 (12.2)		
					3.727	1.361

Table 5.20 Results of CCA on the 39 planktonic diatom species, 40 active sites and 10 environmental variables (EC, Alk, TP, Chla, SD, Na, K, Cl, Ca and Mg). (Numbers in parentheses are individual axis contributions).

Axis	Eigenvalue	Species / environment correlation	Cumulative % variance (species)	Cumulative % variance (species / environment)	Sum of all unconstrained eigenvalues	Sum of all canonical eigenvalues
1	0.326	0.892	8.7	25.6		
2	0.278	0.793	16.2 (7.1)	47.5 (21.5)		
3	0.219	0.746	22.1 (5.9)	64.7 (17.7)		
4	0.160	0.749	26.4 (4.3)	77.3 (13.0)		
					3.727	1.272

Table 5.21 Results of CCA on the 39 planktonic diatom species, 40 active sites and 9 environmental variables (Alk, TP, Chla, SD, Na, K, Cl, Ca and Mg). (Numbers in parentheses are individual axis contributions).

Axis	Eigenvalue	Species / environment correlation	Cumulative % variance (species)	Cumulative % variance (species / environment)	Sum of all unconstrained eigenvalues	Sum of all canonical eigenvalues
1	0.325	0.893	8.7	27.2		
2	0.270	0.788	16.0 (7.0)	49.9 (22.3)		
3	0.218	0.746	21.8 (5.8)	68.1 (18.9)		
4	0.151	0.721	25.9 (4.1)	80.8 (13.0)		
					3.727	1.194

Table 5.22 Results of CCA on the 39 planktonic diatom species, 40 active sites and 8 environmental variables (Alk, TP, Chla, SD, K, Cl, Ca and Mg). (Numbers in parentheses are individual axis contributions).

5.7.4 Forward selection of the remaining environmental variables

A CCA with manual forward selection resulted in five of the remaining eight environmental variables being selected for inclusion in a final CCA (Table 5.23). Mg, Cl and Ca were the three variables eliminated. Following inclusion of Alk, TP, Chla, SD and K in the analysis, Mg, Cl and Ca failed to contribute additional statistically significant explanatory power towards species variation. Further support for the elimination of Cl and Mg is derived from their display of extreme leverage (>2.5 standard deviations from the mean value) in one site

each. Rather than removing two sites from the calibration set, it was deemed more appropriate to remove two environmental variables that could be adequately represented by other intercorrelated variables (i.e. K and Alk). The remaining 5 variables all loaded significantly on either one or both CCA axes 1 and 2. The results of a final CCA constrained to these 5 variables alone are presented in Table 5.24 and Figure 5.12.

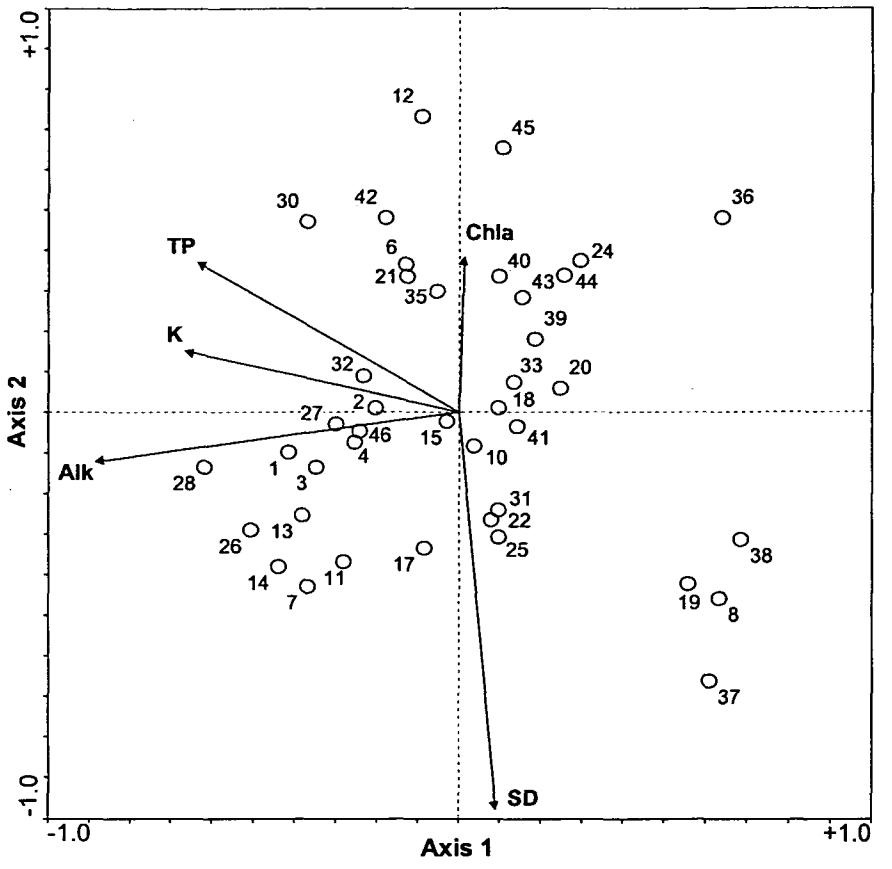
Variable	Order added	Before (marginal effect)	Added (conditional effect)	p-value	% total variance explained
Alk	1	0.279	0.279	0.001	23.4
Mg		0.229			
SD	4	0.224	0.178	0.005	14.9
K	5	0.206	0.141	0.026	11.8
Chla	3	0.199	0.205	0.002	17.2
TP	2	0.198	0.150	0.048	12.6
Cl		0.173			
Ca		0.164			
Total		1.508	0.953 (of 1.194)		79.9

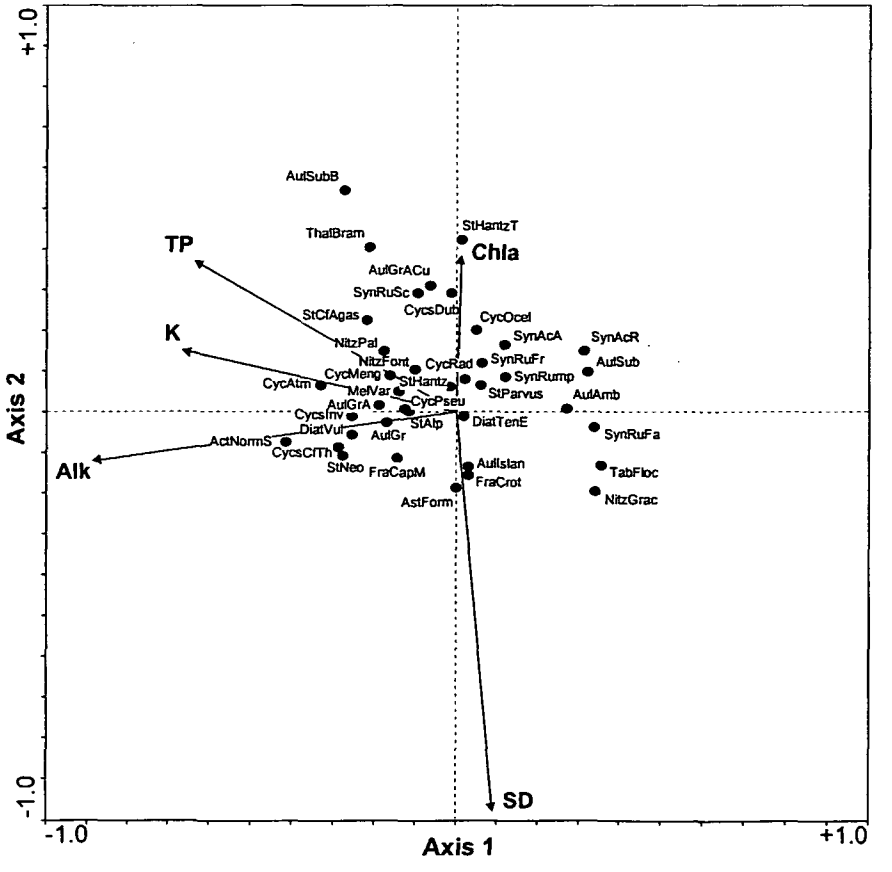
Table 5.23 Results of manual forward selection on the seven remaining environmental variables. Numbers in parentheses indicate the order in which variables were added to the analysis.

Axis	Eigenvalue	Species / environment correlation	Cumulative % variance (species)	Cumulative % variance (species / environment)	Sum of all unconstrained eigenvalues	Sum of all canonical eigenvalues
1	0.300	0.849	8.0	31.5		
2	0.226	0.738	14.1 (6.1)	55.2 (23.7)		
3	0.207	0.729	19.7 (5.6)	77.0 (21.8)		
4	0.120	0.722	22.9 (3.2)	89.5 (12.5)		
					3.727	0.953

Table 5.24 Results of CCA on 39 planktonic diatom species, 40 active sites and 5 environmental variables (Alk, TP, Chla, SD and K). (Numbers in parentheses are individual axis contributions).

The first two axes in the final CCA analysis showed eigenvalues of 0.30 and 0.23 and explained 8.0% and 6.1% of the variance in the diatom species data respectively. The first two axes collectively accounted for 55.2% of the variance in the species-environment relationship, and the species-environment relationship was highly correlated with both CCA axis 1 (0.85) and CCA axis 2 (0.74), indicating the importance of the five variables in explaining variation in the diatom dataset.

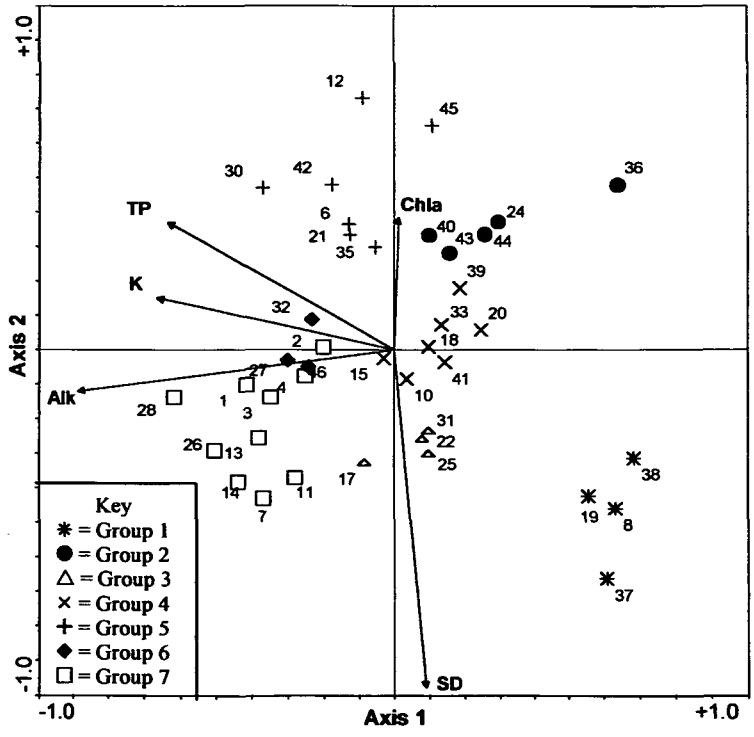




Figures 5.12a & b **CCA tri-plots illustrating five forward selected environmental vectors and a) 40 sites, b) 39 planktonic diatom species.**

5.7.5 CCA site groupings

Figure 5.13 illustrate that the calibration set reservoirs can be delineated into groups. The groupings have not been determined by statistical classification techniques, but instead have been determined by visual means. Since the groupings are for descriptive purposes only and are not carried forward to subsequent analyses, the decision to use visual as opposed to statistical classification methods are thought justified. The visual delineation of clusters is supported in part by the natural group structure within the dataset and also by information of species and environment relationships collected in this study. The resultant clusters enable a logical ecological interpretation to be made.



Figures 5.13 CCA triplot illustrating 5 forward selected environmental vectors and 40 sites grouped according to environmental characteristics and species assemblages (as described in text).

Group 1

Sites located in the lower right quadrant of the ordination plot are characterised by high water clarity but low levels of Alk, K and TP. Sites representing this group include Clatworthy (site 8), Leigh (site 19), Wimbleball (site 37) and Wistlandpound (site 38). These sites are all located on base-poor slate bedrock (except Leigh, which is spring-fed). Species typical of these sites include *T. flocculosa*, *Synedra rumpens v. familiaris*, *Nitzschia gracilis*, *A. ambigua*, *A. subarctica* and *C. radiosa*.

Group 2

Sites positioned in the upper right quadrant of the ordination diagram include Porth (site 24), Upper Tamar (site 36), Arlington (site 40), Darwell (site 43) and Powdermill (site 44). These sites possess below average ionic concentrations, low to moderate TP, but raised Chla concentrations and hence lower than average water clarity. Chelmarsh (site 6) and Trimpley (site 35) may also belong to this group of sites, although they also exhibit similarities with sites / species designated to group 5. Species typical of these sites include *A. subarctica*, *C. radiosa*, *C. dubius*, *A. ambigua*, *A. granulata*, *A. formosa* and *S.* cf. *agassizensis*.

Group 3

A. formosa, *F. crotonensis* and *A. islandica* are typically found in reservoirs which have moderate to high water clarity, moderate to low levels of Chla and moderate concentrations of dissolved ions and TP. Reservoirs exhibiting these characteristics and in which the above species are found, include Hawkridge (site 17), Ogston (site 22), Ravensthorpe (site 25) and Swithland (site 31). These sites are located in the lower quadrants of the ordination diagram, close to the division between left and right quadrants.

Group 4

Cropston (site 10), Foxcote (site 15), Hollowell (site 18), Luxhay (site 20), Tittesworth (site 33), Ardingly (site 39) and Bewl (site 41) are all located close to the centre of the ordination plot, indicating their 'average' (in relation to this data-set) environmental conditions and demonstrating some overlap with many other sites in terms of species assemblages. Species occurring in these reservoirs include *A. subarctica*, *C. radiosa*, *S. parvus*, *A. formosa*, *F. crotonensis*, and *Synedra acus* var. *radians*.

Group 5

This group of sites is positioned predominantly in the upper left quadrant of the ordination diagram. Group members exhibit high algal turbidity, high levels of Chla, low water clarity (low SD) and moderate to high TP and include Durleigh (site 12), Nanpantan (site 21), Sutton Bingham (site 30), Bough Beech (site 42) and Weir Wood (site 45). Chelmarsh (site 6) and Trimpley (site 35) appear to demonstrate characteristics of both this group and group 2. Species associated with these sites include *A. subarctica* fo. *subborealis*, *C. dubius*, *C. radiosa*, *S.* cf. *agassizensis* and *S. hantzschii* (fo. *tenuis*).

Group 6

Located towards the centre of axis 2 and slightly left of centre on axis 1, sites in this group have moderate water clarity, moderate Chla but above average TP, Alk and K. These include Stanford (site 27), Thornton (site 32) and Daventry (site 46). Species occurring in these sites include *A. granulata*, *A. granulata* var. *angustissima* (fo. *curvata*), *Diatoma tenuis* fo. *elongatum*, *S. parvus*, *Cyclostephanos* cf. *tholiformis* and *F. crotonensis*, although this grouping demonstrates considerable overlap with other clusters.

Group 7

Located in the lower left quadrant of the ordination plot, Ardleigh (site 1), Blackbrook (site 2), Blagdon (site 3), Blithfield (site 4), Chew Valley (site 7), Draycote (site 11), Eyebrook (site 13), Foremark (site 14), Rutland (site 26) and Staunton Harold (site 28). These sites show moderate to high alkalinity, K and TP, but are characterised by higher than average water clarity. This may be attributed to the presence of cyanophyte blooms in many of these sites, which allow the penetration of light through colonies despite high nutrient concentrations. Species typical of these sites include *A. normanii* fo. *subsalsa*, *S. neoastraea*, *Diatoma vulgaris*, *C. invisitatus*, *A. granulata* and *A. granulata* var. *angustissima*.

5.7.6 Variance partitioning

Variance partitioning was carried out following the same procedure as with the full dataset (section 5.4.10). Figure 5.14 shows that overall, when Alk is entered in a constrained CCA as the sole environmental variable, it explains the highest proportion of variance in the planktonic diatom distributions (7.49%). However, when a CCA is run with Alk as the only environmental variable and the other four variables as covariables, there is an overlap of 2.38% with both TP and K, leaving a discrete contribution of only 5.11%. Chla and SD explain a lower overall percentage of variance in the species data, but because they display very little overlap with the other variables, their discrete contributions are 5.21% and 5.42% respectively. This result is very similar to that displayed by the full dataset (Figure 5.8) and is unsurprising since SD and Chla exhibit non-significant correlations with most other environmental variables and thus represent largely independent directions of variation in the dataset. The converse is true for Alk, TP and K, because in common with the full dataset, these variables derive a moderate to high proportion of their explanatory power from the effects of covariance.

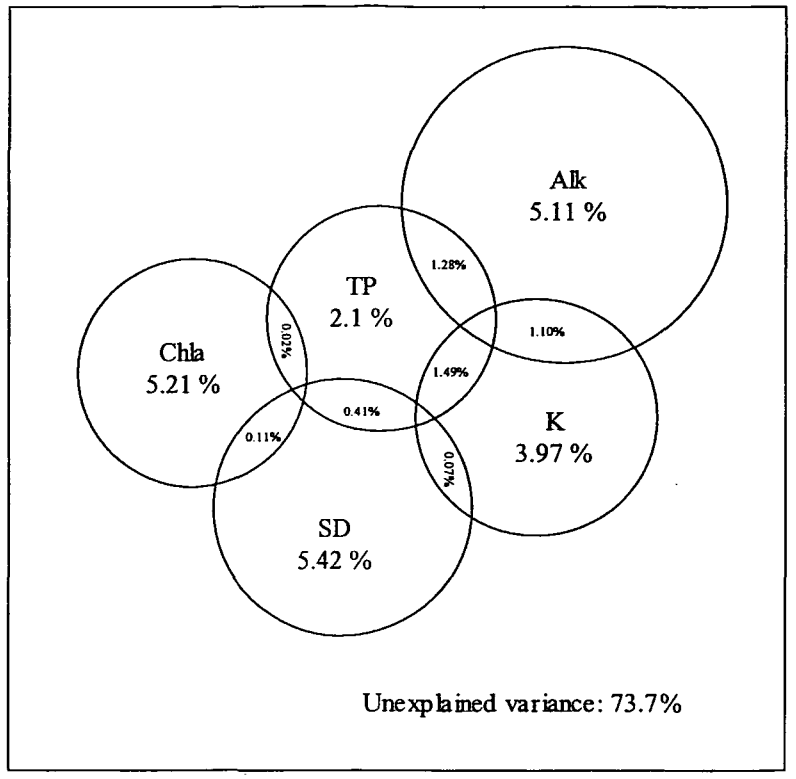


Figure 5.14 Variance partitioning of the 40 reservoir planktonic dataset. Diatom species variation is partitioned into that which is independently explained by individual measured environmental variables (non-overlapping portions of circles), that which co-varies between variables (overlap) and that which is unexplained by the measured variables (the remainder). Circles are proportional to total variance explained (unexplained variance and overlap between circles not proportional).

5.8 Summary points

- Planktonic diatoms dominate the lowland reservoir surface sediment assemblages (mean percentage relative abundance = 78% of the total assemblage). Results of ordination analyses on both the full and planktonic datasets indicate that due to the dominance of planktonic diatoms, the explanatory power of the planktonic dataset is similar to that comprising both planktonic and periphytic taxa. This justifies the subsequent development of a planktonic calibration dataset and inference models in addition to those based on the full dataset.
- There are two main axes of variation in the diatom species data shown by CCA – axis 1 is a water chemistry gradient, representing both nutrient and ionic concentrations. Axis 2 is a water clarity gradient, which in part reflects algal productivity.
- Constrained CCAs showed that of the measured environmental variables, Alk, EC, TP, Chla, SD and K explained the greatest amount of variation in the surface sediment diatom species assemblages of both the full and planktonic UK lowland

reservoirs datasets. Therefore, these variables are considered suitable for the development of diatom-based inference models.

- The species gradients shown in DCA for both full (2.92 and 2.59 SD units for axes 1 and 2 respectively) and planktonic (3.16 and 2.47 SD units for axes 1 and 2 respectively) datasets are sufficient to assume that most species responses can be approximated by unimodal models. This supports the use of unimodally based methods i.e. weighted averaging (WA) regression and calibration, in the development of diatom-based inference models.

CHAPTER SIX

Diatom plankton seasonality

6.1 Introduction

It has been demonstrated that individual planktonic diatom species often exhibit clear seasonal growth preferences (Reynolds, 1984b). To maximise the value of planktonic diatom data in palaeolimnological research, an understanding of modern species distributions, interactions and ecology is vital (Kilham *et al.*, 1996; Bradshaw & Anderson, 2002). Sayer (1997, 2001) demonstrated that surface sediment diatom assemblage composition was dependent upon the seasonality of individual planktonic diatom species. In particular he found that there was an overrepresentation in the surface sediments of those taxa comprising the most recent diatom bloom. This chapter examines diatom plankton seasonality, which should increase the understanding of contemporary diatom species ecology in the UK lowland reservoirs calibration dataset. This aids interpretation of species shifts in the palaeolimnological records analysed in the current study, but should also be applicable in other similar palaeolimnological studies, particularly at sites where the plankton provides the dominant habitat for diatom growth (Sayer and Roberts, 2001; Bradshaw *et al.*, 2002).

This chapter illustrates the seasonality of planktonic diatom species in 9 selected reservoirs – Blackbrook, Chew Valley, Clatworthy, Hawkridge, Hollowell, Porth, Sutton Bingham, Tittesworth and Upper Tamar. Site selection was based on i) planktonic life forms dominating the diatom flora, ii) the presence of planktonic diatoms throughout the sampling period, iii) characterisation by a broad range of diatom taxa and iv) representation of sites along the trophic gradient. Sites were visited on seven separate occasions over an 18-month period between May 1999 and October 2000. Epilimnetic diatom plankton samples and an associated suite of contemporary limnological variable data were collected and analysed for each sampling period.

For each of the nine sites, seasonal data for key environmental variables and graphical representations of seasonal diatom plankton and surface sediment diatom assemblage data are presented. For sites where Water Company data for other algal groups were available, these are presented alongside. Individual DCA ordination diagrams are also presented for each of the nine sites. These diagrams illustrate trajectories followed by the seasonal diatom

plankton samples and the position of the surface sediment diatom assemblages in relation to these.

Data were analysed using both Detrended Correspondence Analysis (DCA) and Canonical Correspondence Analysis (CCA) to investigate differences and similarities between sites and seasons. A DCA ordination diagram is presented for the nine reservoirs, where the seasonal plankton samples have been entered as 'active' in the analysis. This enables comparison of the seasonal diatom assemblages present in each reservoir and the extent of overlap between the species assemblages occurring in different sites. CCA ordination is also used to interpret the interplay between seasonal successional sequences in species assemblages and environmental data both between and within sites. The seasonality of diatom species assemblages in individual reservoirs and the differences and similarities in seasonal species shifts between different reservoirs are interpreted in light of the available literature.

The same DCA ordination of all nine reservoirs is re-presented with the surface sediment and modern planktonic assemblages entered as 'passive'. This allowed determination of the degree of difference between 'live' and fossil diatom assemblages, and in turn provided useful taphonomic data as well as an indication of an individual reservoir's current sediment accumulation rate. Further, for three selected reservoirs different depth 'surface' sediment samples were compared (0-0.5 cm, 0.5-1 cm and 1-2 cm). The percentage relative abundance of different diatom taxa were determined and the floristic composition of each depth sample was compared with both the floristic composition and proportional representation of diatom taxa in the seasonal plankton samples. This provided useful information on the most appropriate time to sample surface sediments and the surface sediment depth that gave the best approximation of an individual reservoir's most recent, annually integrated diatom plankton assemblage.

6.2 Seasonality of planktonic diatoms and environmental variables

On a site-by-site basis this section discusses the seasonal trends in key environmental variables and diatom plankton assemblages for each of the nine reservoirs. Pie charts are presented to illustrate the seasonality of the dominant planktonic diatom taxa (percentage relative abundance data) and line graphs display the seasonality of key environmental variables. For sites where Water Company data were available, line graphs are presented to illustrate the seasonality of different algal groups, namely diatoms, chlorophyta and cyanophyta. Pie charts are also presented to illustrate the composition of the surface

sediment diatom assemblages. Comparisons are drawn between the assemblages recorded in the 'live' seasonal plankton samples and those documented in the sediment record.

The dates when samples were taken from individual reservoirs may not always fall within the months listed for each sample period. This is particularly true of the September 2000 plankton and water chemistry samples, some of which were taken in October 2000 due to logistical constraints. The majority of surface sediment samples were taken in September/October 2000, but samples for two of the reservoirs, namely Sutton Bingham and Upper Tamar were taken in June 2000, again for logistical reasons. The exact sampling dates for plankton / water chemistry and surface sediment samples are discussed in the text for individual sites and noted adjacent to their respective pie charts.

In common with the data used to construct the pie charts, the species data used in the DCA ordinations are based on the percentage relative abundance of individual diatom taxa. Thus, positioning of the diatom taxa on the ordination diagrams is influenced by species composition and not by overall cell concentrations. To determine the cell contributions of individual taxa recorded in each season and hence their relative weightings, it is necessary to examine the line graphs illustrating seasonal diatom cell concentrations in conjunction with the compositional data.

Individual DCA ordination diagrams for each of the nine reservoirs are displayed. Only the seasonal plankton samples are 'active' in each analysis. Samples from successive seasons are connected using straight lines to show trajectories between the different seasonal diatom plankton assemblages. Alongside these, the 'surface' sediment planktonic diatom assemblages are plotted passively.

6.2.1 Blackbrook

Figures 6.1 and 6.2 display seasonal data for Blackbrook reservoir. Chla and Temp follow similar seasonal trends, showing their lowest levels in the winter and peaking in the summer. Si concentrations follow the inverse trend of Chla and Temp, peaking in the winter and early spring and showing their lowest concentrations in the summer. There appears to be a close inverse relationship between Si and diatom biovolumes / cell concentrations. Si reaches a peak prior to the onset (and at the start) of a diatom bloom (e.g. July 1999 and March 2000), but Si concentrations then decrease markedly throughout and subsequent to the bloom (e.g. July 1999 and June 2000), suggesting that there is a substantial Si uptake by the blooming diatom population.

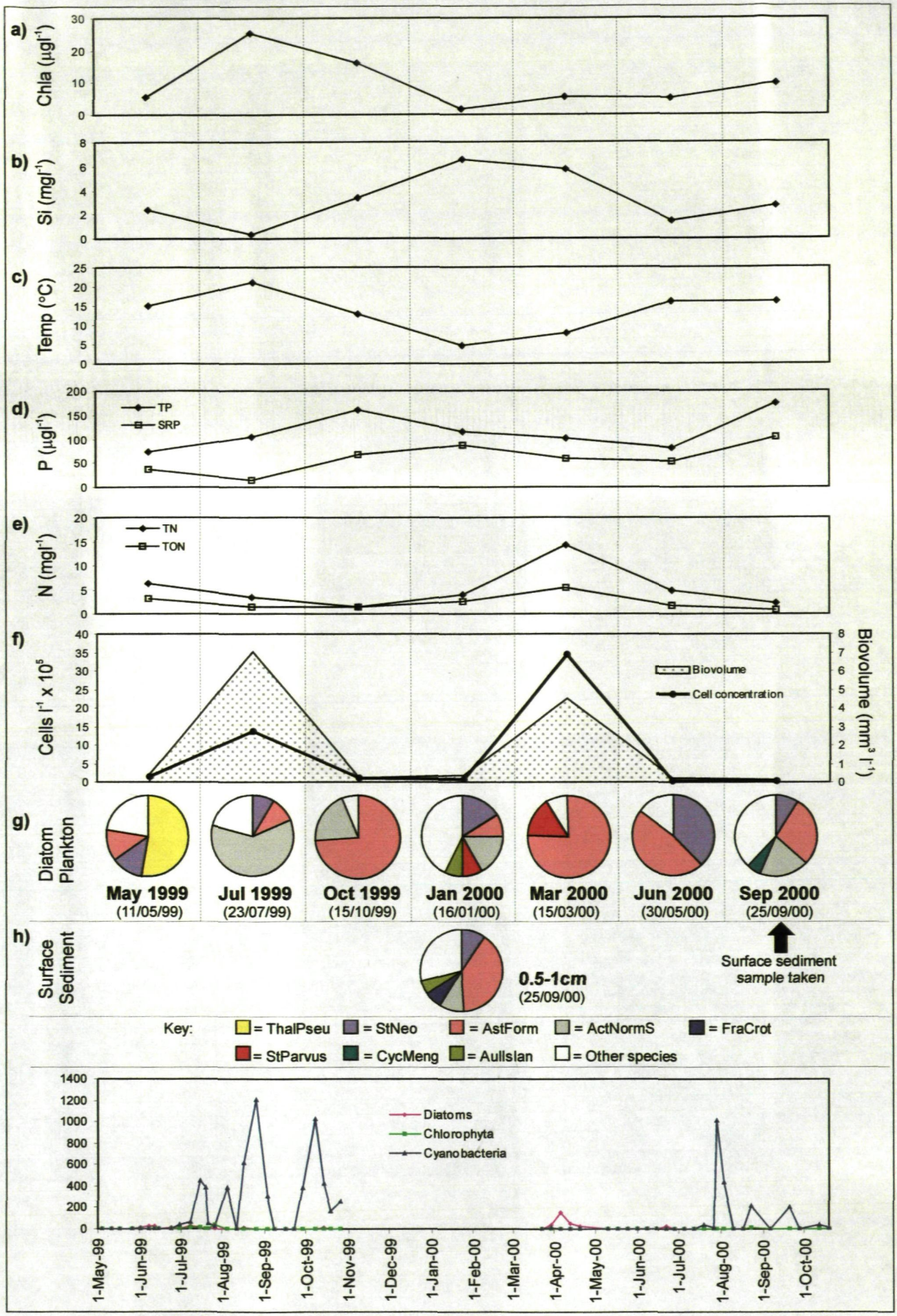


Figure 6.1 **Blackbrook Reservoir; Seasonal data for key environmental variables (a-e), diatom cell concentrations and biovolumes (f), diatom plankton assemblages (g), surface sediment diatom assemblage (h), and algal concentrations (STW) (i).**

TP and SRP concentrations follow similar overall trends, as do TN and TON. Blackbrook does not appear to be P-limited, except perhaps in July 1999. SRP is at its lowest concentrations in July 1999, possibly reflecting the high P-demand of the large centric diatoms *Actinocyclus normanii* fo. *subsalsa* and *Stephanodiscus neoastraea*, or that of the cyanophytes and/or chlorophyta present in the water column at this time. TP rises throughout the summer, probably reflecting the high algal biomass consisting predominantly of cyanophytes. Biologically available concentrations of N (TON) remains relatively stable, rising slightly in March 2000 in tandem with TN, which reaches a peak at this time. The seasonal pattern of decreasing concentrations of TON throughout the spring and summer is probably attributable to increased rates of assimilation by algae during the growing season, a pattern frequently observed by other authors e.g. Bennion & Smith (2000).

Blackbrook was dominated by cyanophytes during the late summer to autumn period in both 1999 and 2000 (up to ~1200 cells l^{-1} $x10^5$). The water was loaded with cyanophytes throughout these periods. This may help to explain the restricted seasonality of the diatom blooms since large cyanophyte blooms can, through 'self-shading', limit light availability for the growth of other algal groups (Reynolds, 1984b). Furthermore, this may explain the very low diatom cell concentrations (<2 cells l^{-1} $x10^5$) and biovolumes (<0.25 mm^3 l^{-1}) in the May 1999 and June 2000 plankton samples.

It is apparent from the Severn Trent Water (STW) algal data (Figure 7.3i) that the diatom blooms at Blackbrook are relatively short-lived and as a consequence easy to miss in a coarse sampling programme such as that pursued in the current study. For example, in July 1999 there was a diatom bloom consisting predominantly of *A. normanii* fo. *subsalsa*. This bloom was picked up in the current study. However a small diatom bloom recorded by STW in late June 2000 appears to have been overlooked because the June 2000 sample (taken 30/5/00) showed very low diatom cell concentrations, as did the September 2000 sample (taken 25/9/00).

Diatoms appear to bloom in the greatest concentrations in the spring. The pennate taxon, *Asterionella formosa* dominates and the small centric taxon, *Stephanodicus parvus* occurs as a subdominant. In the summer, both prior to cyanophyte dominance and at times of lower cyanophyte cell concentrations, the large centric diatoms *A. normanii* fo. *subsalsa* and to a lesser extent *S. neoastraea*, form a major component of the diatom population. These taxa

probably depleted the water of remaining Si and contribute to large diatom biovolumes but only moderate cell concentrations.

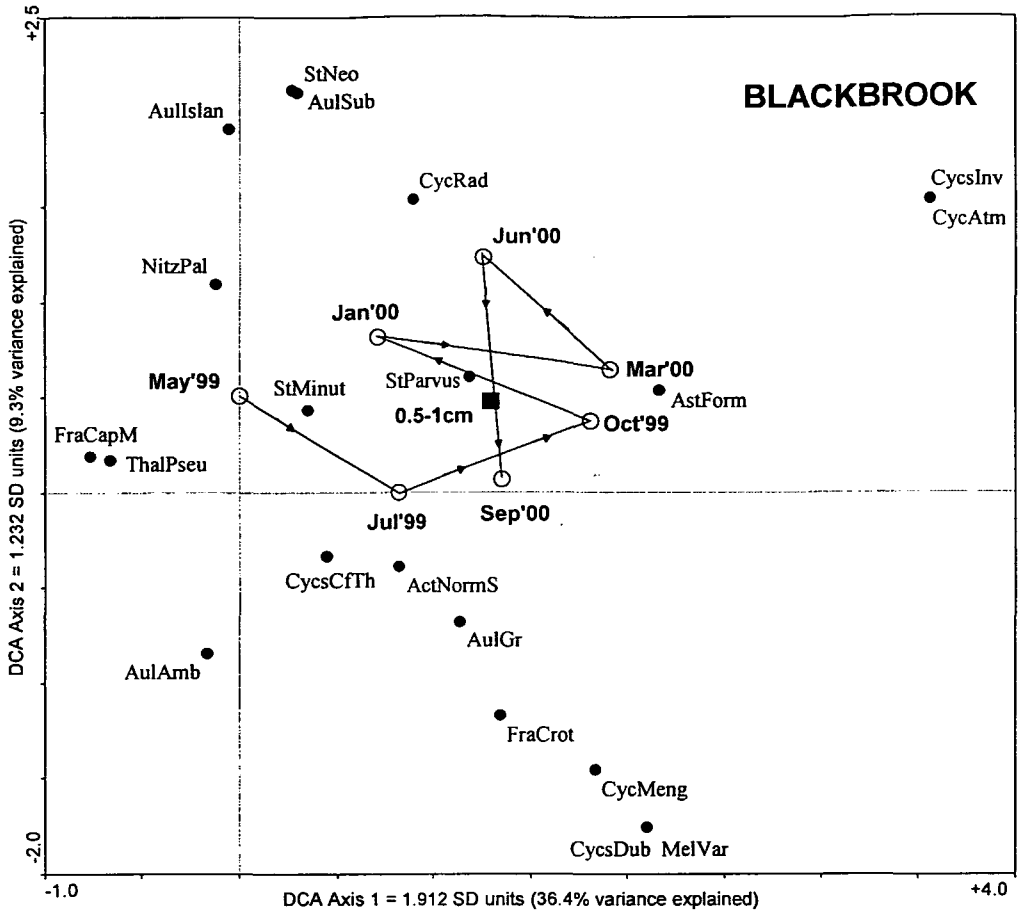


Figure 6.2 DCA ordination diagram illustrating Blackbrook reservoir's seven seasonal diatom plankton samples (active - open circles) and the 0.5-1 cm surface sediment planktonic diatom assemblage (passive – black square). For species codes see Appendix 3.

The May 1999 sample is the most distinct in terms of species composition. Despite showing overall low cell concentrations, this sample is dominated by a high relative abundance of the tiny centric diatom *Thalassiosira pseudonana*, which greatly influences the positioning of the May 1999 sample on the ordination diagram (Figure 6.2). The July 1999 sample is composed predominately of *A. normanii* fo. *subsalsa*, with relatively little *A. formosa*, which places this sample close to *A. normanii* fo. *subsalsa* on the ordination plot. The March 2000 and October 1999 samples lie in close proximity, both comprising approximately 75% *A. formosa*, with the remainder composed predominantly of *S. parvus* and *A. normanii* fo. *subsalsa* respectively. The 0.5-1 cm surface sediment planktonic diatom assemblage lies mid-way between the seasonal samples in the ordination space. This indicates that, based on the data collected in this study, the surface sediment assemblage provides a good overall representation of the floristic composition of planktonic diatom

species occurring in Blackbrook reservoir's plankton over the previous 12-18 month period. However, the high relative abundance of *T. pseudonana* that occurs in the May 1999 plankton sample is absent from the 0.5-1 cm surface sediment sample. This may occur because i) *T. pseudonana* is a small and weakly silicified diatom taxon (<5 μm diameter and ~50 μm^3 biovolume) and may thus readily dissolve before incorporation into the fossil record; ii) Blackbrook has either a fast or very slow sedimentation rate and thus the 0.5-1 cm sediment sample has failed to capture the May 1999 bloom of *T. pseudonana*; or iii) the high percentage relative abundance of *T. pseudonana* in the May 1999 sample gives a false impression of the overall contribution this taxon to fossil assemblage, since it only occurs in one seasonal plankton sample at low cell concentrations and biovolumes. *Fragilaria crotonensis* is present in the 0.5-1 cm sediment sample, but occurs at a lower relative abundance in those seasonal samples in which it occurs. This could be because i) the coarse resolution seasonal plankton sampling has failed to capture a significant seasonal bloom of *F. crotonensis*; or ii) *F. crotonensis* is more resistant to dissolution and breakage in the period prior to incorporation into the fossil record, thus increasing its relative abundance in the fossil assemblage.

6.2.2 Chew Valley

Figure 6.3 displays the seasonality data for Chew Valley reservoir. Chla concentrations appear to be closely associated with the diatom cell concentrations and biovolumes measured in this study. Temperature also follows a similar trend. Unlike the trends seen in many other reservoirs, Si concentrations are not closely related to temperature. Si is present in rather low overall concentrations, which appears to be directly related to the predominance of diatoms in Chew's water column. During the period of low diatom cell concentrations between March 2000 and June 2000, Si concentrations increase to a peak of ~4 mgl^{-1}, but decrease to 0 mgl^{-1} by 7/10/00 following a substantial diatom bloom. This suggests that Si in seasonally limiting diatom growth in Chew Valley.

Chew Valley also appears to be N-limited throughout the summer and autumn, although there is a dramatic recovery in TON concentrations over the winter and early spring when phytoplankton concentrations are low. This reservoir is generally rich in available P (SRP) and is not thought to be P-limited at any time during the year. For example in September 2000 both Si and TON concentrations are at 0 mgl^{-1}, whereas there remains sufficient SRP available for plant growth.

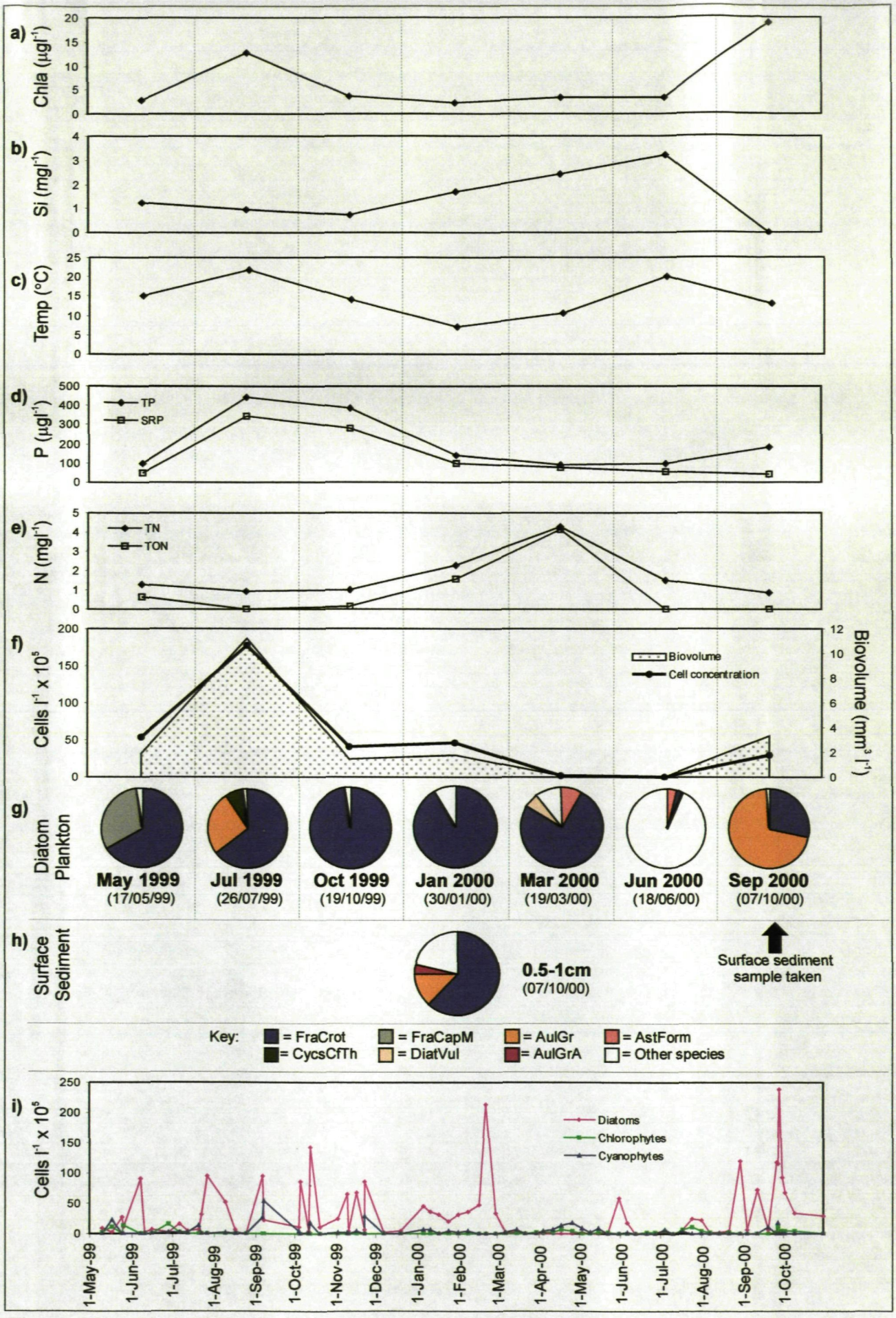


Figure 6.3 **Chew Valley Reservoir; Seasonal data for key environmental variables (a-e), diatom cell concentrations and biovolumes (f), diatom plankton assemblages (g), surface sediment diatom assemblage (h), and algal concentrations (BWW) (i).**

Diatoms are the dominant algal group present in Chew Valley, forming substantial populations throughout the year. The dominant taxon is *F. crotonensis*, which occurs with *A. formosa* in the spring, *Fragilaria capucina* var. *mesolepta* in the early summer and *Aulacoseira granulata* during late summer. Unfortunately in both March 2000 and June 2000, the diatom blooms recorded by Bristol Water Works (BWW) occurred prior to the time of sampling in this study. The March 2000 plankton sample is thought to consist of remnants of the earlier sustained bloom. The June 2000 plankton sample showed very low diatom cell concentrations and is composed mainly of epiphytic diatom taxa, possibly reflecting an increase in macrophyte host species at this time. Also present are some planktonic diatom remnants from the small, short-lived bloom that occurred in early June 2000. Similarly, the September 2000 sample (actually taken on 7/10/00), fails to capture four individual peaks in diatom cell concentrations (up to ~250 cells l^{-1} $x10^5$). This could explain why *Aulacoseira granulata* var. *angustissima* is absent from the seasonal plankton samples, whilst it occurs at ~3% in the 0.5-1 cm surface sediment sample. *F. capucina* var. *mesolepta*, *Cyclostephanos* cf. *tholiformis* and *A. formosa* are present in the 0.5-1 cm surface sediment sample, but only at relative abundances of <1%. These species appear in the seasonal plankton at relative abundances of up to 30%, however the dominance of *F. crotonensis* and *A. granulata* in the plankton over the sampling period reduces the relative abundance of these taxa, resulting in apparent low species diversity in the fossil assemblage. This suggests that square root transformation of species data may be useful to prevent the loss of ecological information during the development of inference models.

Figure 6.4 illustrates the trajectory followed by the seasonal diatom plankton assemblages in Chew Valley reservoir. The planktonic diatom assemblages recorded in October 1999, January 2000 and March 2000 are very similar, lying close together in ordination space due to their shared domination by *F. crotonensis*. The positioning of the May 1999 sample is influenced by the subdominance of *F. capucina* var. *mesolepta*, whilst the location of the July 1999 and September 2000 samples are influenced by the presence of *A. granulata*. The June 2000 sample is dominated by non-planktonic taxa, the only planktonic taxa present being *A. formosa* and *F. crotonensis*, occurring at low percentage relative abundance. Consequently, the position of the June 2000 sample lies approximately mid-way between these two taxa. Both the 0.5-1 cm and 1-2 cm 'surface' sediment samples also lie in close proximity, influenced by the domination of *F. crotonensis*. The composition of the 0-0.5 cm sample is mid-way between those of the July 1999 and September 2000 plankton samples. The presence of a high relative abundance of *A. granulata* in both the September 2000 plankton sample and the 0-0.5 cm sediment sample (taken on 7/10/00) may indicate that the

0-0.5 cm sample is an artefact of the most recent diatom plankton bloom. The significance of this will be discussed further in section 6.7.

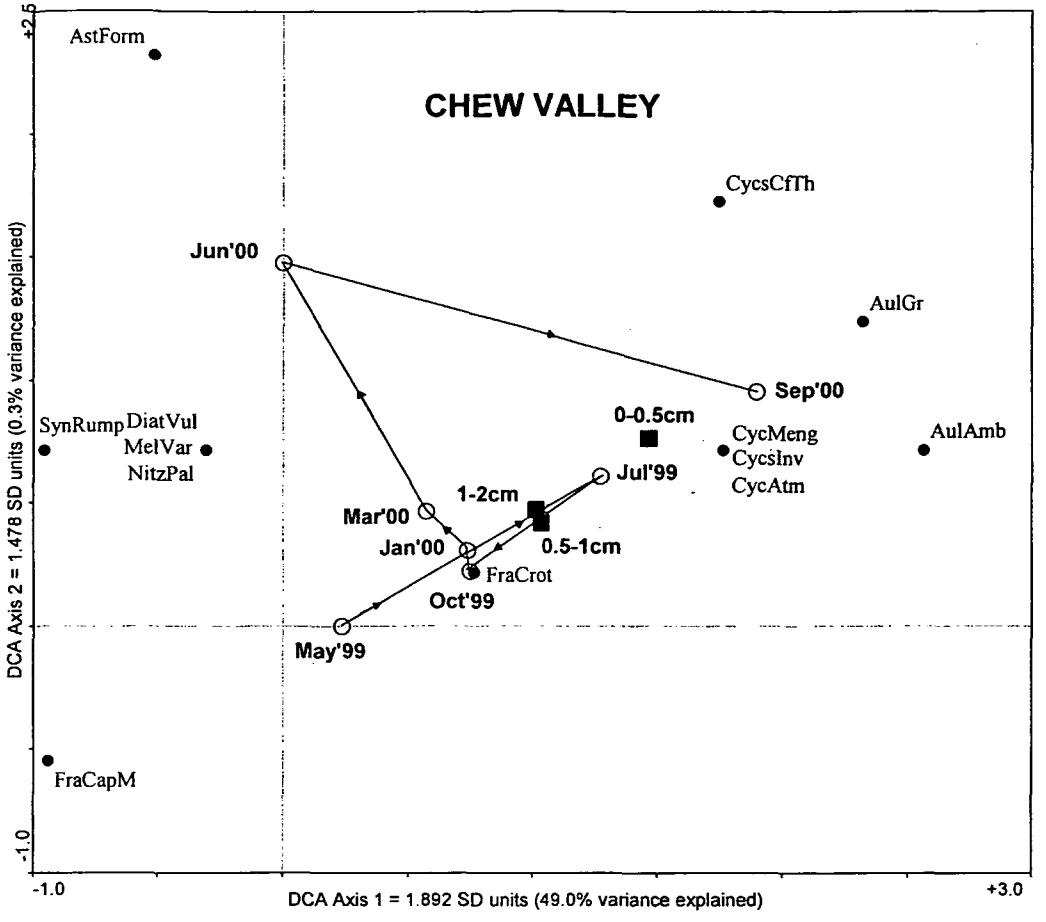


Figure 6.4 DCA ordination diagram illustrating Chew Valley reservoir's seven seasonal diatom plankton samples (active – open circles) and the 0-0.5 cm, 0.5-1 cm and 1-2 cm sediment planktonic diatom assemblages (passive – black squares). For species codes see Appendix 3.

6.2.3 Clatworthy

Figure 6.5 displays the seasonal data for Clatworthy reservoir. Clatworthy supports a reasonably diverse range of planktonic diatom taxa throughout the year, although diatom cell concentrations and biovolumes remain consistently low (<10 cells l^{-1} x10^5 and <0.3 mm^3 l^{-1} respectively) compared to those seen in most other sites. The main exception is the single-species bloom of *F. crotonensis* seen in June 2000, when diatom cell concentrations peak at ~40 cells l^{-1} x10^5. Si concentrations are also at their lowest during the summer, recovering during the autumn and winter, to coincide with the period of lowest water temperatures.

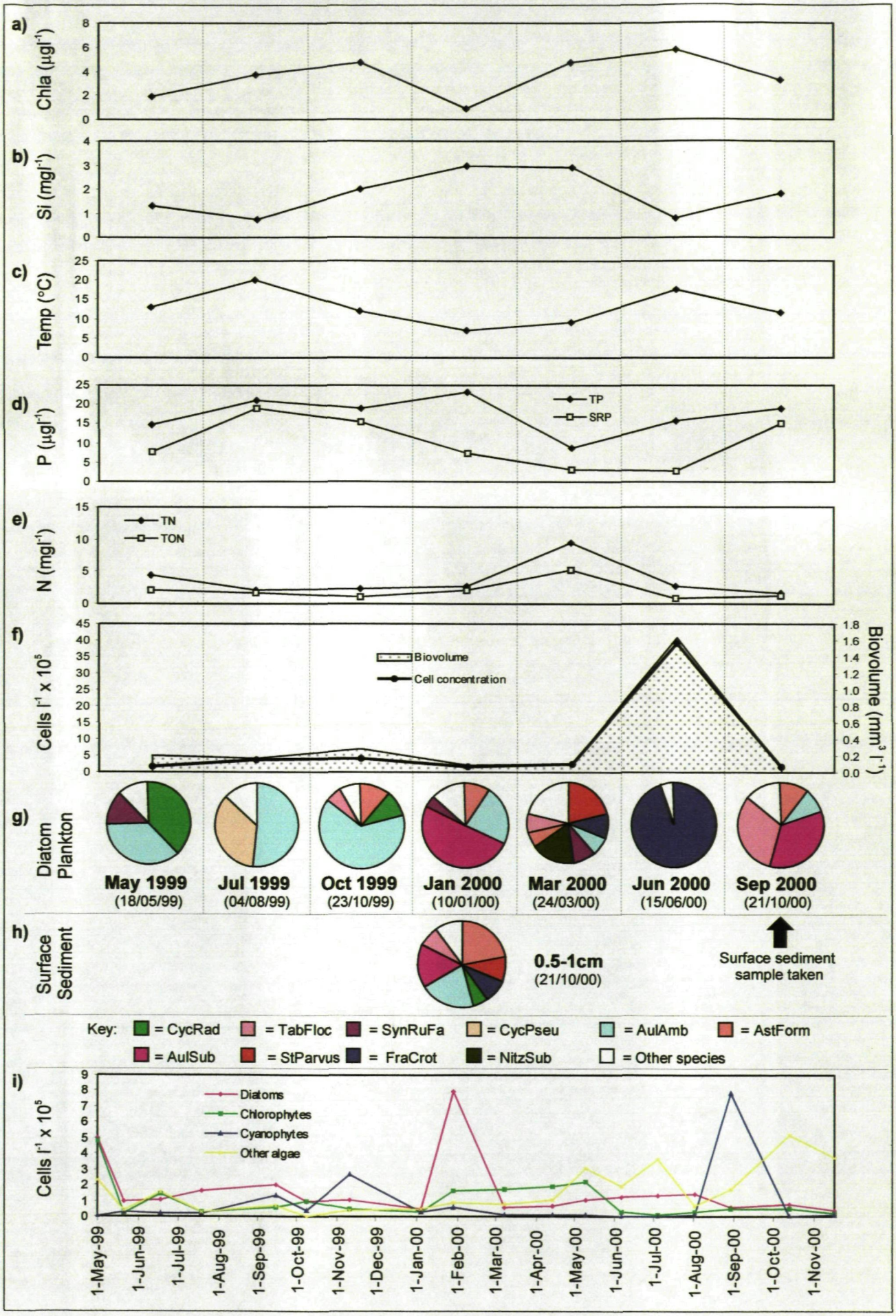


Figure 6.5 **Clatworthy Reservoir; Seasonal data for key environmental variables (a-e), diatom cell concentrations and biovolumes (f), diatom plankton assemblages (g), surface sediment diatom assemblage (h) and algal concentrations (WW) (i).**

The diatom taxon seen in greatest relative abundance in 1999 is *Aulacoseira ambigua*, although *Cyclotella radiosa*, *Cyclotella pseudostelligera*, and to a lesser extent *Synedra rumpens* var. *familiaris*, *A. formosa* and *Tabellaria flocculosa* are also recorded over this period. In January 2000, when Si is at its highest concentration and Temp is low, *Aulacoseira subarctica* accounts for ~50% of the diatom population. In March 2000, *Nitzschia subacicularis* and *S. parvus* co-dominate, replacing *A. subarctica*, perhaps in response to increasing SRP assimilation. In September 2000 (sample actually taken 21/10/00), both *A. subarctica* and *T. flocculosa* co-dominate, with the same subdominants as seen in January 2000. These taxa appear to out-compete *F. crotonensis* when water temperature is low, but have a broader tolerance for both SRP and Si. They survive successfully in both high and low Si and SRP environments, but are unable to compete successfully with *F. crotonensis* as water temperature increases beyond ~15°C. This observation is supported by Reynolds *et al.* (1983), who reported that the growth dynamics of *F. crotonensis* may be satisfied at higher light levels, thus dominance of the spring-blooming taxa were not threatened. The bloom of *F. crotonensis* occurs when TON and Si

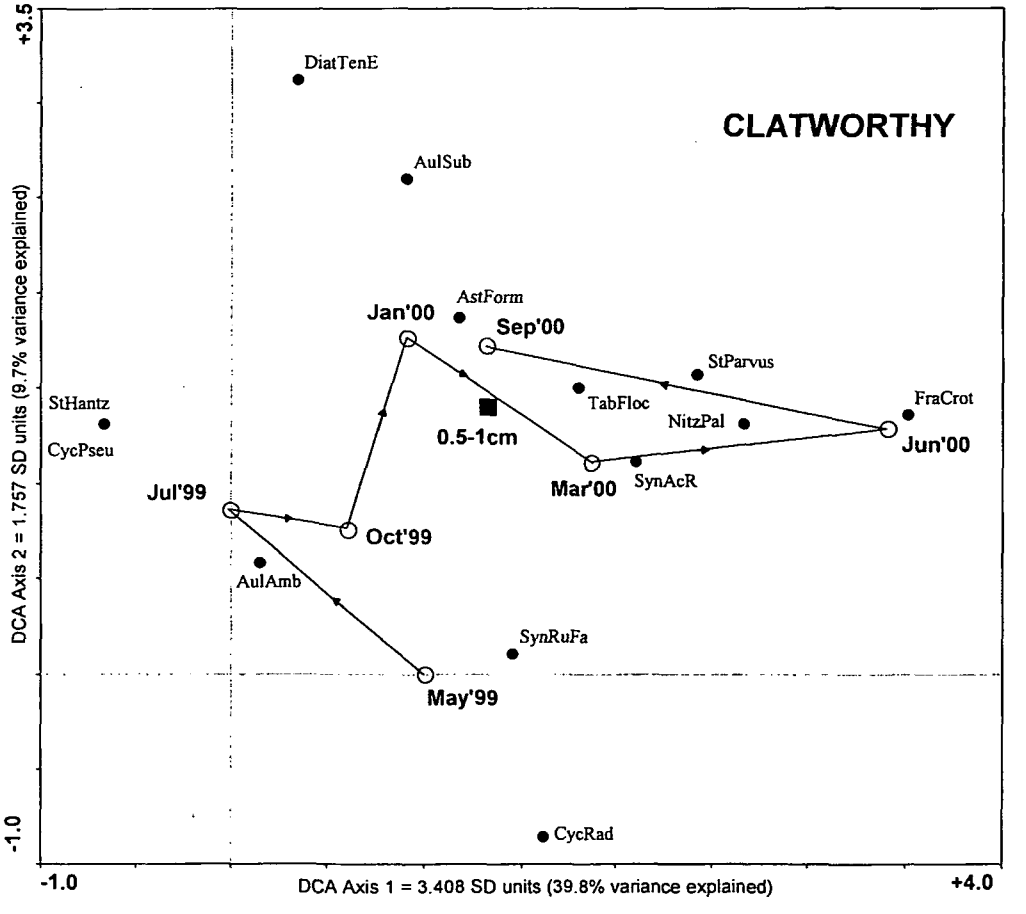


Figure 6.6 **DCA ordination diagram illustrating Clatworthy reservoir's seven seasonal diatom plankton samples (active – open circles) and the 0.5-1 cm surface sediment planktonic diatom assemblage (passive – black square). For species codes see Appendix 3.**

concentrations are high, SRP is low and temperature is rising, suggesting that *F. crotonensis* is competitive in these conditions, displacing taxa blooming earlier in the season such as *A. subarctica*, *A. ambigua* and *S. parvus*.

Figure 6.6 illustrates the trajectory followed by the seasonal diatom plankton assemblages in Clatworthy reservoir. The May 1999, July 1999 and October 1999 plankton samples comprise a high percentage relative abundance of *A. ambigua* and consequently are positioned in relatively close proximity to *A. ambigua*. *A. subarctica* dominates the January 2000 and September 2000 plankton samples and the positioning of these samples largely reflects the high relative abundance of *A. subarctica*. The March 2000 plankton sample is extremely diverse, with seven taxa occurring at >5% relative abundance, locating this sample in a central position on the ordination diagram. The 0.5-1 cm sediment sample is also located centrally, indicating that this fossil assemblage has captured the floristic diversity of the recently sedimented planktonic diatom populations. However, since the main diatom bloom recorded in this study is dominated by *F. crotonensis*, and the 0.5-1 cm sample only comprises ~10% *F. crotonensis*, it is suggested that Clatworthy's sedimentation rate is relatively slow in comparison to sites such as Chew Valley and that the June 2000 *F. crotonensis* bloom would probably have dominated the 0-0.5 cm sample. Alternatively the plankton samples taken in this study have failed to capture populations of other taxa blooming in the intervening periods that make up the 0.5-1 cm sediment sample.

6.2.4 Hawkridge

Figure 6.7 displays the seasonal data for Hawkridge reservoir. Similar to most other reservoirs, Si concentrations in Hawkridge increase over the cool winter and early spring period, when diatom cell concentrations are also at their lowest levels. TON follows a similar seasonal trend to that recorded in most other reservoirs, showing increasing concentrations throughout the winter and early spring, with the lowest concentrations occurring during the main season of phytoplankton growth.

Chla concentrations are overall rather low, only rising markedly during the summer and autumn of 2000, to coincide with diatom blooms dominated by *F. crotonensis*. Over the same period, Si concentrations decrease, becoming undetectable by September 2000, indicating that the bloom of *F. crotonensis* has assimilated all the available Si from the water column. SRP concentrations are at their lowest during this period (1-7 μgl^{-1}), indicating that *F. crotonensis* has the ability to compete successfully under conditions of low available P, as seen in Clatworthy.

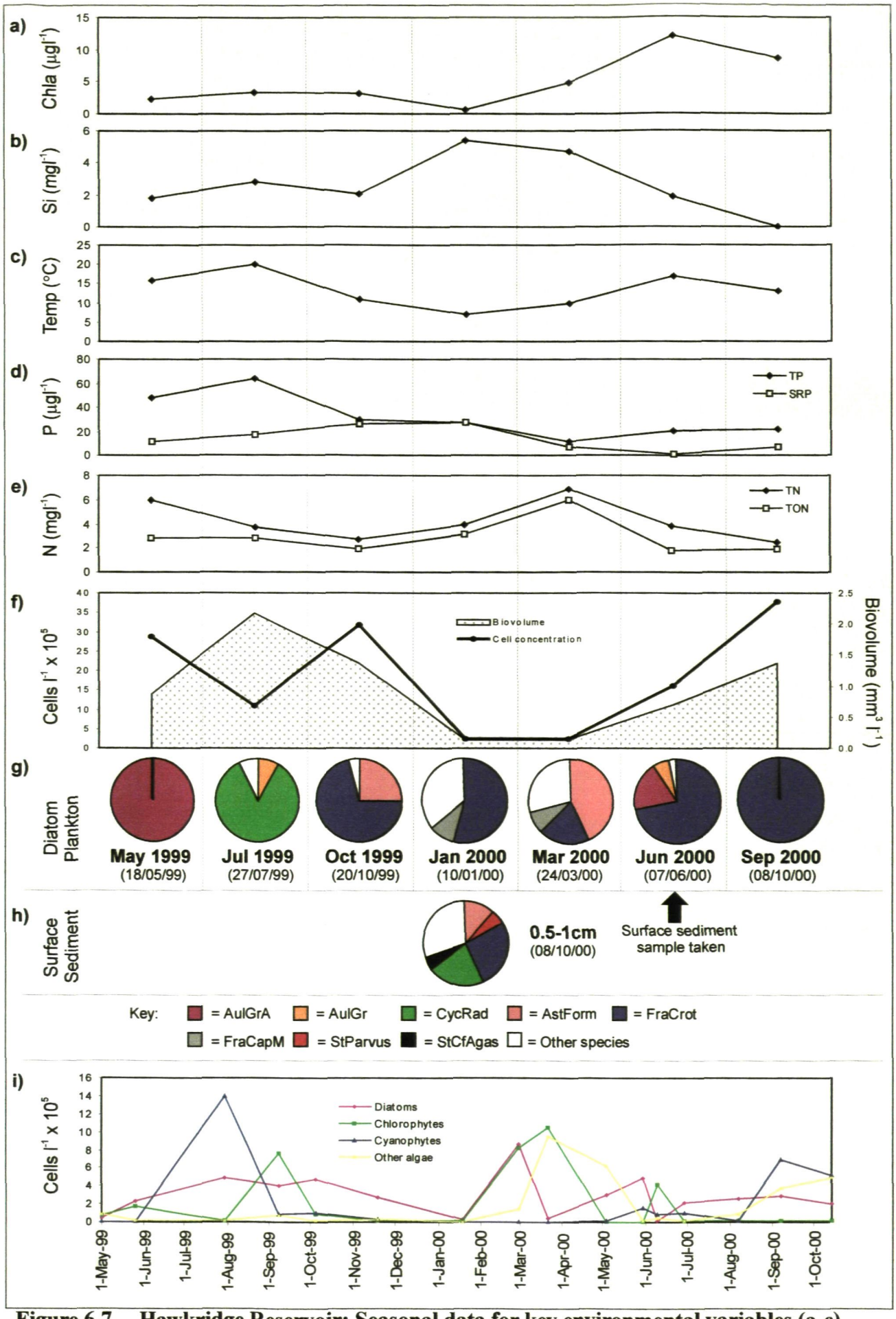


Figure 6.7 **Hawkridge Reservoir; Seasonal data for key environmental variables (a-e), diatom cell concentrations and biovolumes (f), diatom plankton assemblages (g), surface sediment diatom assemblage (h) and algal concentrations (WW) (i).**

In both May 1999 and June 2000, there is a bloom of *A. granulata* var. *angustissima*. This dominates the diatom assemblage in May 1999, but occurs as a subdominant to *F. crotonensis* in June 2000. In July 1999, when water temperature is at its highest (20°C), *C. radiosa* dominates the diatom assemblage. Increasing TP and TN concentrations at these times, mirrored by increasing diatom biovolumes, may indicate that the phosphorus assimilated in the cells of the *C. radiosa* population is the main contributor to measured TP at this time. *A. formosa* and *F. capucina* var. *mesolepta* occur in the coolest months (October to March) when SRP and Si concentrations are moderate to high and TON is increasing. *Stephanodiscus* cf. *agassizensis* is present in the surface sediment sample (5%), but was absent from the seasonal plankton samples. A bloom of *S.* cf. *agassizensis* may not therefore have been captured by the coarse sampling frequency employed in this study.

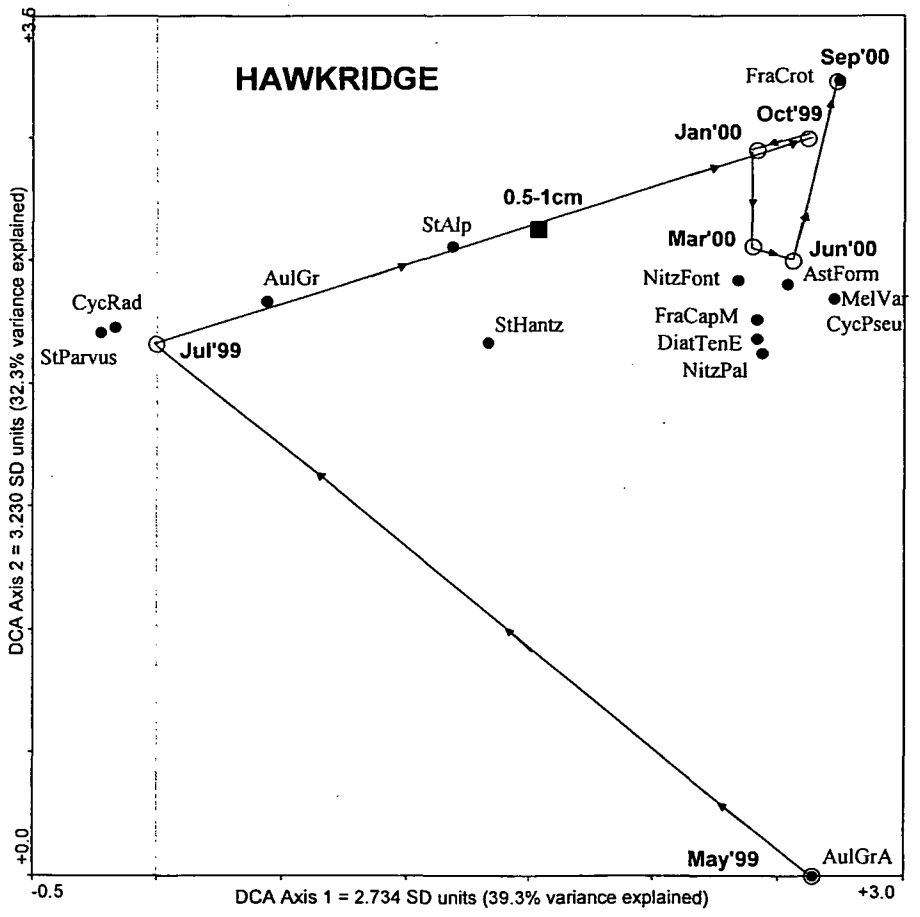


Figure 6.8 DCA ordination diagram illustrating Hawkridge reservoir's seven seasonal diatom plankton samples (active – open circles) and the 0.5-1 cm surface sediment planktonic diatom assemblage (passive – black square). For species codes see Appendix 3.

Figure 6.8 illustrates the trajectory followed by the seasonal diatom plankton assemblages in Hawkridge reservoir. The May 1999 and July 1999 plankton samples are dominated by *A. granulata* var. *angustissima* and *C. radiosa* respectively, taxa that occur at a high relative

abundance only in these samples. The May 1999 and July 1999 samples are thus distanced from the other seasonal plankton samples in ordination space. The diatom assemblages of plankton samples taken in October 1999 – September 2000 are positioned in relatively close proximity on the ordination diagram. High relative abundances of *F. crotonensis* primarily influence the location of these samples, whilst *A. formosa* and *A. granulata* var. *angustissima* provide a secondary influence on the ordination of the March 2000 and June 2000 samples respectively. The 0.5-1 cm sediment sample comprises 21% *C. radiosa*, 25% *F. crotonensis* and 12% *A. formosa*, which determine its position in ordination space. The 0.5-1 cm sample is located between the seasonal samples for July 1999 and March 2000, indicating that the diatom plankton present during this period is the most representative of the assemblage present in the 0.5-1 cm sediment sample. This is reinforced by the absence in the 0.5-1 cm sample of *A. granulata* var. *angustissima*, which occurs at a significant relative abundance only in May 1999 and June 2000.

6.2.5 Hollowell

Figure 6.9 displays the seasonal data for Hollowell reservoir. Hollowell shows overall moderately low Chla concentrations (<7 μgl^{-1}), only rising to 25 μgl^{-1} when diatom cell concentrations and biovolumes increase in September 2000 during a bloom dominated by *Cyclostephanos invisitatus*. Hollowell appears to be both P and Si-limited. Si concentrations are also low and appear to be rapidly exhausted by diatom blooms e.g. in March 2000 and September 2000. Alongside the commonly observed winter recovery in Si concentrations, there also appears to be a recovery in April – May 2000, which coincides with a period of cyanophyte domination in the plankton. There is however no corresponding summer recovery of SRP, indicating that competition for SRP between algal groups is intense at Hollowell.

Hollowell supports a diverse range of diatom taxa, with *C. radiosa*, *F. crotonensis*, *Cyclostephanos dubius*, *A. formosa* and *C. invisitatus* dominating the diatom assemblage in different seasonal samples. Only *F. crotonensis* and *A. formosa* predominate during more than one season (July and March, and January and June respectively). Blooms of *F. crotonensis* appear to coincide with low Si and SRP concentrations, a phenomenon also seen in Hawkridge and Clatworthy reservoirs. However uncertainty surrounds whether the *F. crotonensis* blooms are the cause of, or a response to, low Si and SRP concentrations. This is difficult to assess based on the coarse seasonal data collected in this study, although the available literature suggests the former (Tilman *et al.*, 1982). *C. radiosa* dominates

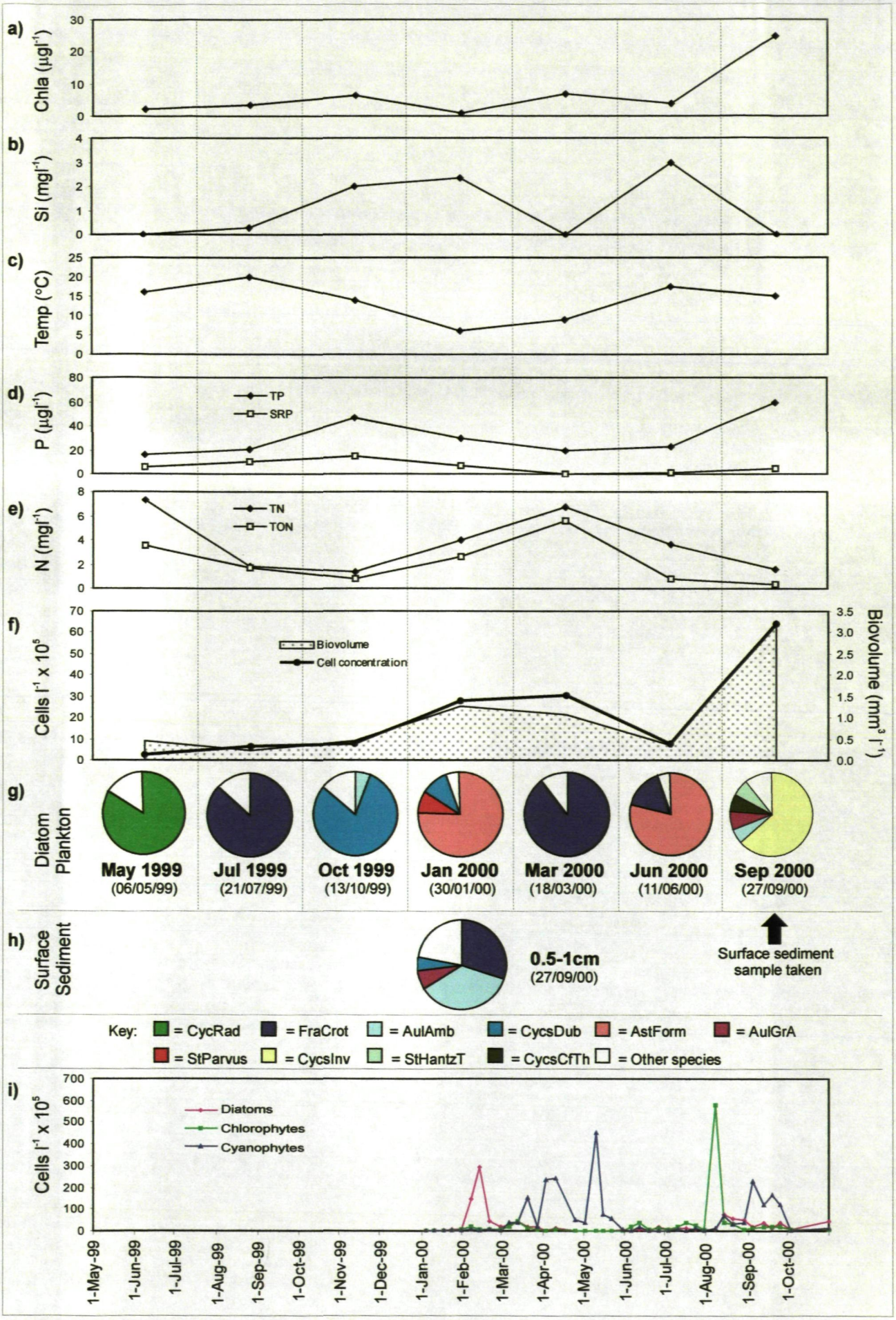


Figure 6.9 **Hollowell Reservoir; Seasonal data for key environmental variables (a-e), diatom cell concentrations and biovolumes (f), diatom plankton assemblages (g), surface sediment diatom assemblage (h), and algal concentrations (AW) (i).**

during May 1999 when Temp, TON and SRP concentrations are relatively high, and Si concentrations are low. This seasonal preference is similar to that seen by Sayer in shallow Norfolk lakes (pers. comm.). *C. dubius* dominates (with *A. ambigua* as a subdominant) in October 1999, when SRP is high and TON is low. In the following year, *C. invisitatus* dominates the assemblage, with overall diatom cell concentrations higher in September 2000 than in any other seasonal sample. *C. invisitatus* survives alongside a large cyanophyte bloom in September 2000, perhaps indicating that this taxon is highly competitive under conditions of low SRP and low light availability. This taxon clearly dominates the September 2000 plankton sample, occurring at the highest cell concentrations seen over the sampling period (~65 cells l^{-1} $x10^5$), suggesting that the plankton sampling captured a bloom of *C. invisitatus*. However, *C. invisitatus* is absent from the surface sediment sample. This appears to support the decision to analyse 0.5-1 cm surface sediment samples as opposed to 0-0.5 cm slices, the latter of which may have over-represented the latest seasonal bloom of *C. invisitatus*.

According to the Anglian Water (AW) algal data, the largest diatom bloom occurred in February 2000, the onset of which may have been captured in this study's January 2000 plankton sample. If this is the case, the bloom is composed primarily of *A. formosa*, a taxon with moderate Si and P requirements. *S. parvus* also occurs, but at a low percentage relative abundance. On the whole, Hollowell displays low concentrations of Si, possibly confining taxa such as *A. formosa* to the Si-rich waters of the winter/early spring period. The dominance of *A. formosa* in June may coincide with the activation of destratification equipment at the site, perhaps increasing Si concentrations in the water column through resuspension of Si from the sediment (Bailey-Watts, 1986).

Figure 6.10 illustrates the trajectory followed by the seasonal diatom plankton assemblages in Hollowell reservoir. Due to the diverse rapidly altering seasonal diatom assemblages seen in Hollowell's plankton, seasonal samples are widely scattered in the ordination diagram. This is further highlighted by the long axis lengths of both DCA axis 1 (3.775 S.D. units) and DCA axis 2 (3.244 S.D. units). The May 1999 plankton sample is the only sample dominated by *C. radiosa* and therefore is positioned away from the other taxa and samples towards the extreme left of the diagram. For similar reasons of single species dominance the other samples are well scattered. The July 1999 and March 2000 samples are located close to *F. crotonensis*, the October 1999 sample is positioned alongside *C. dubius*, the January 2000 and June 2000 samples are positioned close to *A. formosa* and the September 2000 sample lies in close proximity to *C. invisitatus*.

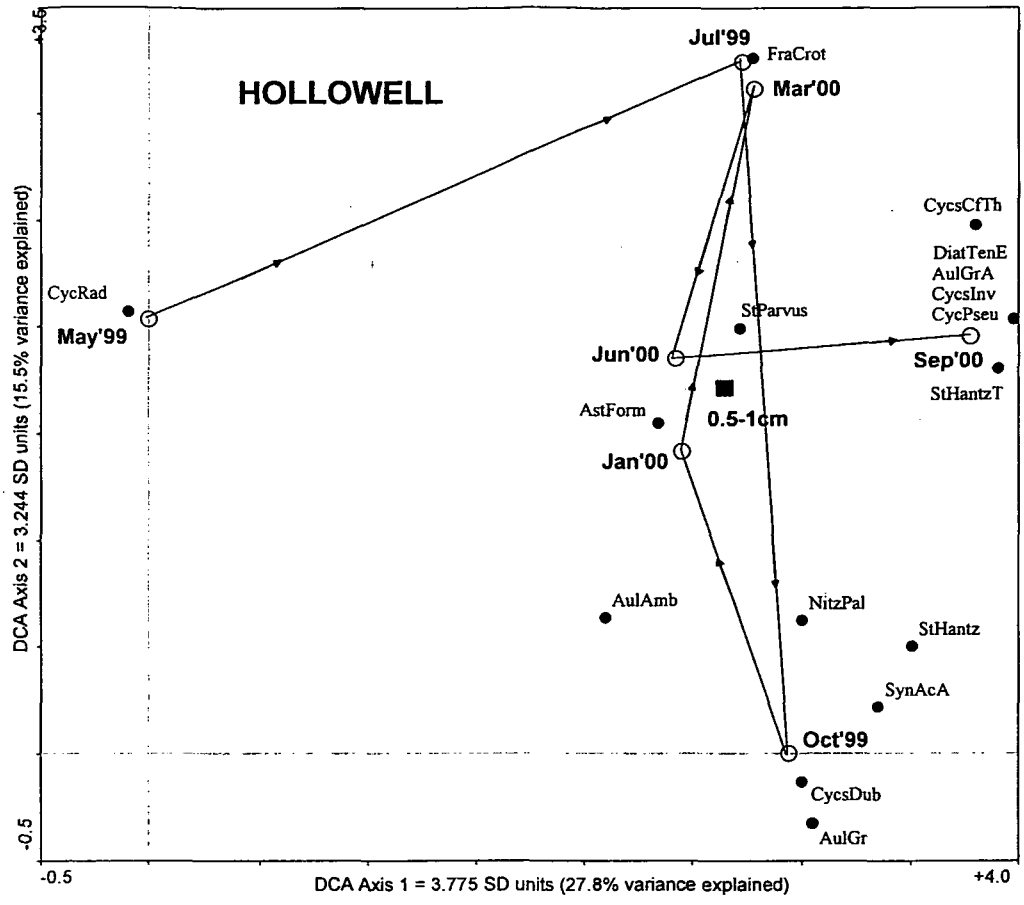


Figure 6.10 DCA ordination diagram illustrating Hollowell reservoir's seven seasonal diatom plankton samples (active – open circles) and the 0.5-1 cm surface sediment planktonic diatom assemblage (passive – black square). For species codes see Appendix 3.

The 0.5-1 cm sediment sample is positioned in a relatively central position. This is not because the assemblage present in this sample is similar to those seen in the plankton in January 2000 and June 2000, or indeed those present in the mean plankton samples. The position of the 0.5-1 cm sample is dictated by its composition of 38% *A. ambigua* and 32% *F. crotonensis*, which places it mid-way between these taxa when plotted passively in the DCA ordination. The percentage relative abundance of *A. ambigua* in the 0.5-1 cm sediment sample is considerably higher than the maximum percentage of *A. ambigua* recorded in any seasonal plankton sample collected from Hollowell in the course of this study (6.3% in October 1999). This suggests that either the coarse plankton sampling in this study has failed to capture a seasonal bloom of *A. ambigua*, or that the reservoir has a slow sedimentation rate and that the 0.5-1 cm sediment sample was laid down prior to the commencement of plankton sampling in May 1999. Based on the observation that Hollowell reservoir is dominated by short-lived, often single-species diatom blooms, it is thought that the former explanation is more realistic.

6.2.6 Porth

Figure 6.11 displays the seasonal data for Porth reservoir. Porth appears to be P-limited, since SRP concentrations are consistently extremely low. Conversely TON concentrations are generally high, and it is not thought that Porth is N-limited at any time. The supply of Si to the water column also appears to be plentiful, enabling the growth of substantial diatom blooms. Subsequent to large diatom blooms, Si concentrations decrease markedly, increasing the competitive advantage of the lower Si-demanding taxa such as *C. dubius* and *C. radiosa* (Tilman *et al.*, 1982).

Porth's diatom assemblage exhibits a clear seasonality. The reservoir is dominated by *A. subarctica*, the main bloom of which occurs in the spring (March 2000 cell concentrations ~200 cells l^{-1} $x10^5$). The Chla peak appears to follow the main diatom bloom period, probably indicating that diatoms are the dominant algal group living in Porth's phytoplankton. *C. dubius* dominates the summer diatom assemblage with *C. radiosa* occurring alongside in both July 1999 and June 2000 but at a lower relative abundance. *A. formosa* and *A. ambigua* occur at low relative abundance in the summer months 1999 and 2000 respectively. *A. granulata* appears to bloom only in the autumn period, occurring at ~3% in October 1999 and at 71% in September 2000 (28/10/00). *C. radiosa* and *A. ambigua* only occur in the surface sediment sample at relative abundances of <2%, despite being present in summer plankton assemblages at 10-20%. The larger cell concentrations of the dominant spring-blooming taxon (*A. subarctica*) reduce the relative abundance of the summer-blooming taxa in the surface sediment sample.

Figure 6.12 illustrates the trajectory followed by the seasonal diatom plankton assemblages in Porth reservoir. Since Porth's seasonal diatom plankton assemblage is dominated by *A. subarctica* between Oct'99 and Jun'00, these plankton samples all lie in close proximity to *A. subarctica* on the ordination plot. The May 1999 plankton sample is dominated by *C. dubius* and is positioned in the bottom left quadrant of the ordination plot close to where *C. dubius* is located. The September 2000 sample is dominated by *A. granulata*, therefore this sample is positioned close to *A. granulata* towards the right-hand side of the ordination diagram. The position of the July 1999 sample towards the mid-left of the diagram is influenced largely by its proportion of *C. dubius*, but also by the proportions of the subdominant taxa *C. radiosa*, *A. subarctica* and *A. formosa*.

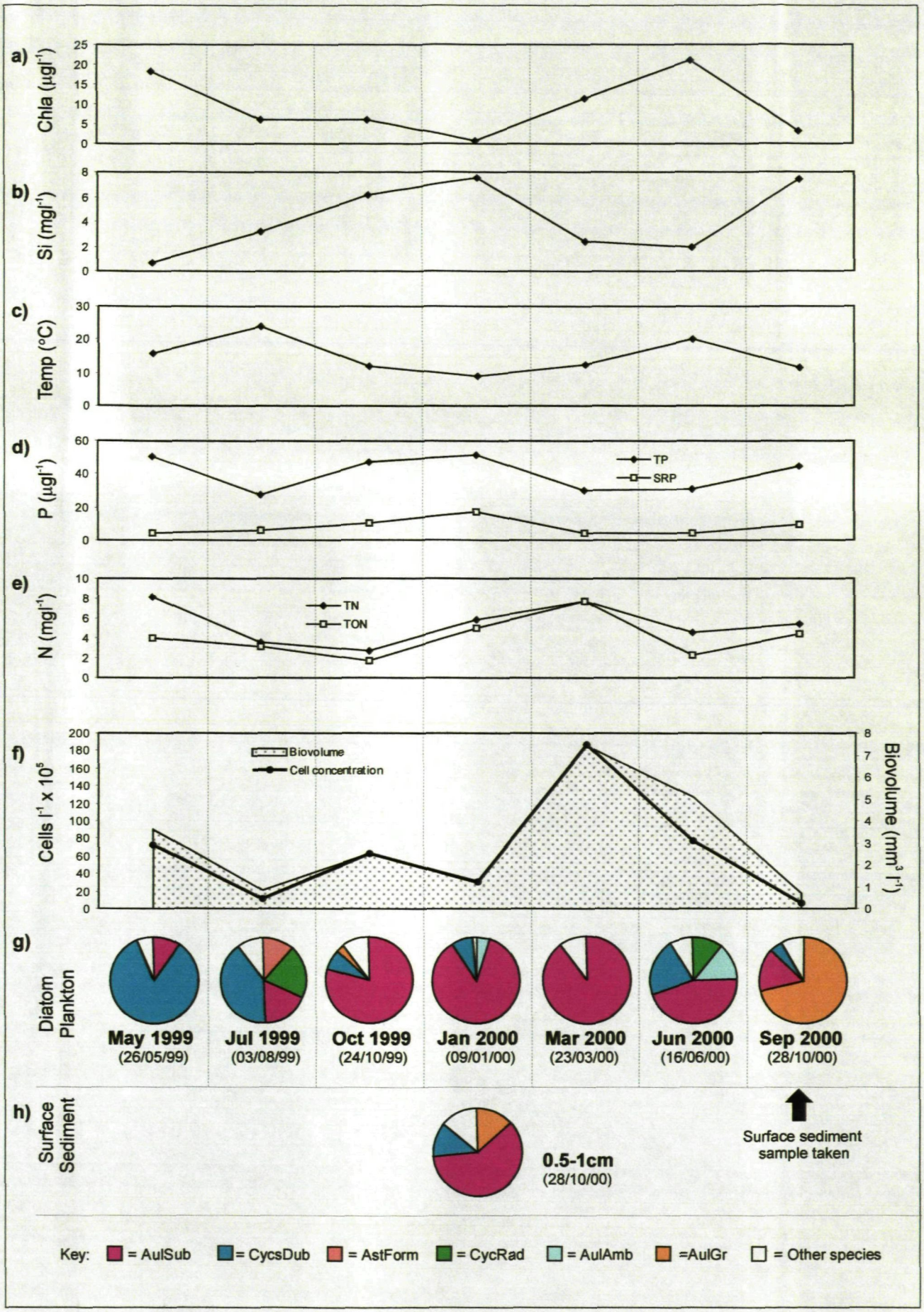


Figure 6.11 Porth Reservoir; Seasonal data for key environmental variables (a-e), diatom cell concentrations and biovolumes (f), diatom plankton assemblages (g), surface sediment diatom assemblage (h).

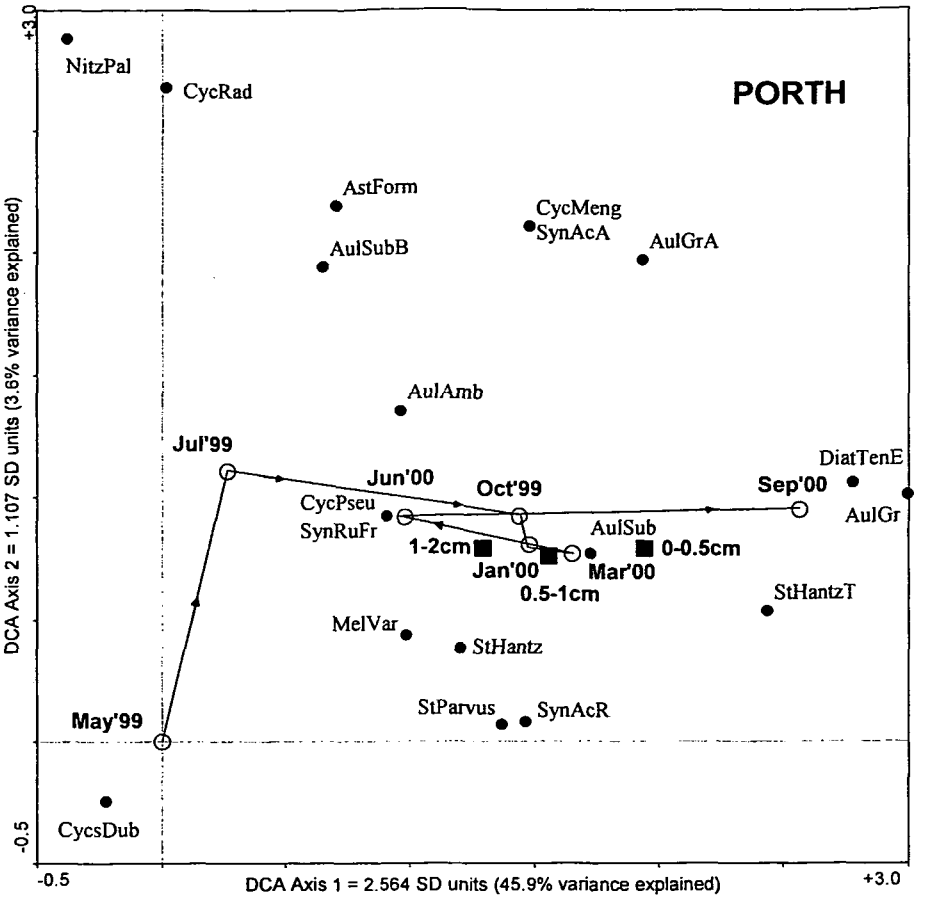


Figure 6.12 DCA ordination diagram illustrating Porth reservoir's seven seasonal diatom plankton samples (active – open circles) and the 0-0.5 cm, 0.5-1 cm and 1-2 cm sediment planktonic diatom assemblages (passive- black squares). For species codes see Appendix 3.

The 0.5-1 cm sediment sample lies in very close proximity to the centre of the ordination and *A. subarctica*, indicating that the 0.5-1 cm fossil assemblage shows a good representation of the contemporary community. The 0-0.5 cm sediment sample lies to the right of the centre, closer to the September 2000 plankton sample, reflecting the relatively high proportion of *A. granulata*, a significant component of the most recent seasonal plankton bloom. The 1-2 cm sample is drawn slightly toward *C. dubius* and away from *A. granulata*, which is only present in a very low abundance in this sample. These observations will be discussed further in section 6.7.

6.2.7 Sutton Bingham

Figure 6.13 displays the seasonal data for Sutton Bingham. Chla concentrations peak twice during the time period covered by this study, once in July 1999 and then more significantly in March - June 2000. Unfortunately Wessex Water's (WW) algal data are only measured monthly, making it difficult to assess the exact timing and extent of the algal blooms. From the data available, the July 1999 peak in Chla concentrations appears to coincide with a

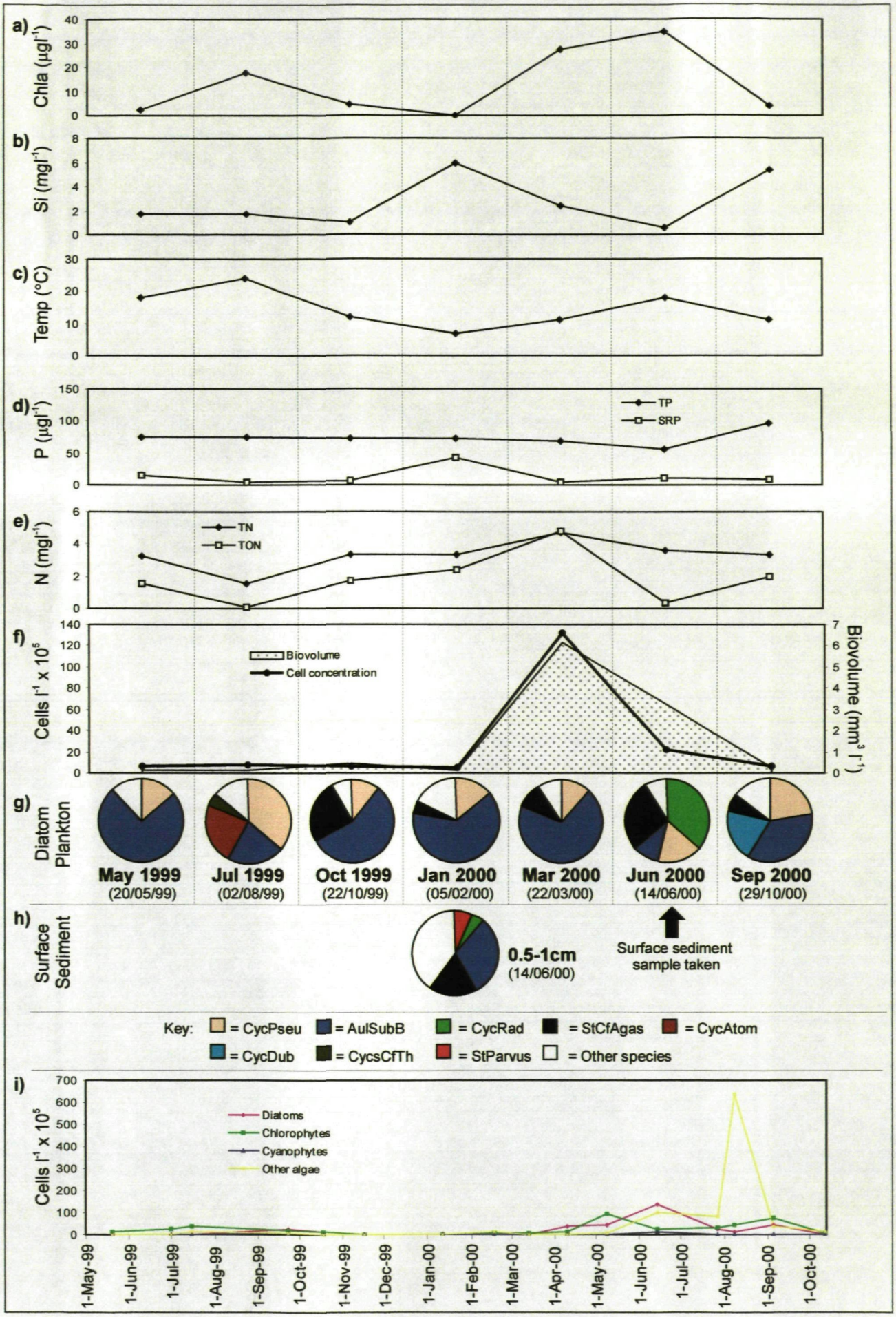


Figure 6.13 Sutton Bingham Reservoir; Seasonal data for key environmental variables (a-e), diatom cell concentrations and biovolumes (f), diatom plankton assemblages (g), surface sediment diatom assemblage (h), and algal concentrations (WW) (i).

peak in chlorophyta, whilst the March 2000 and June 2000 peak appears to result from a combined diatom and chlorophyta bloom. These peaks in Chla are mirrored by decreases in TON to its lowest levels in July 1999 and June 2000 (0.1 and 0.4 mgl^{-1} respectively). This could provide evidence that Sutton Bingham becomes N-limiting during periods of high phytoplankton productivity.

As with other sites, Si and SRP are utilised over the growing season and then recharged during the winter months. Si concentrations are low from May to October 1999, but recover over the winter period in 1999. Similar recovery occurs in September 2000, which could be the result of very windy weather at this time stimulating sediment resuspension and hence raising concentrations of Si in the water column of this relatively shallow reservoir (cf. Bailey-Watts *et al.*, 1989a,b). Once recharged, this Si is then utilised by blooming diatoms, such as that seen in March 2000, dominated by *Aulacoseira. subarctica* fo. *subborealis* (cf. Denys *et al.*, 2003). A bloom of both *C. radiosa* and *S.* cf. *agassizensis* follows this in June 2000, reducing Si concentrations to levels comparable with those seen in 1999 (~0.5 μgl^{-1}). During late July and August 2000, low Si, TON and SRP concentrations all have the potential to limit diatom growth, perhaps increasing the competitive advantage of chlorophyta at this time. Similarly, from May 1999 to August 2000 chlorophyta dominate in low Si, TON and SRP conditions. Cyanophyta do not contribute significantly to Sutton Bingham's algal populations, perhaps because the TN:TP ratio remains moderate and relatively constant, perhaps providing unfavourable conditions for cyanophytes to successfully out compete other algal groups.

Cyclotella atomus and *C. radiosa* occur only in the summer months (July 1999 and June 2000) and although *C. pseudostelligera* is present in all seasons, it is present at its highest relative abundance during the summer. *C. dubius* occurs predominantly in September 2000 (sample actually taken 29/10/00), although as seen in Porth, this may be a taxon that actually bloomed in the period between June and September.

Figure 6.14 illustrates the trajectory followed by the seasonal diatom plankton assemblages in Sutton Bingham reservoir. Since the majority of seasonal plankton samples are dominated by *A. subarctica* fo. *subborealis*, the May 1999, October 1999, January 2000 and March 2000 samples occur in the centre of the ordination diagram, in close proximity to this taxon. The July 1999 sample is located slightly above the centre of the ordination space, lying between *C. pseudostelligera* and *C. atomus*, taxa co-dominating this sample alongside *A. subarctica* fo. *subborealis*. The June 2000 sample is positioned to the right of the

ordination space due to its co-dominance by *C. radiosa* and *S.* cf. *agassizensis,* which lie towards the right of the ordination diagram. The September 2000 sample is positioned above the central cluster due to the two subdominant species contained in this sample, *C. pseudostelligera* and *C. dubius*, which occur towards the top of the ordination space.

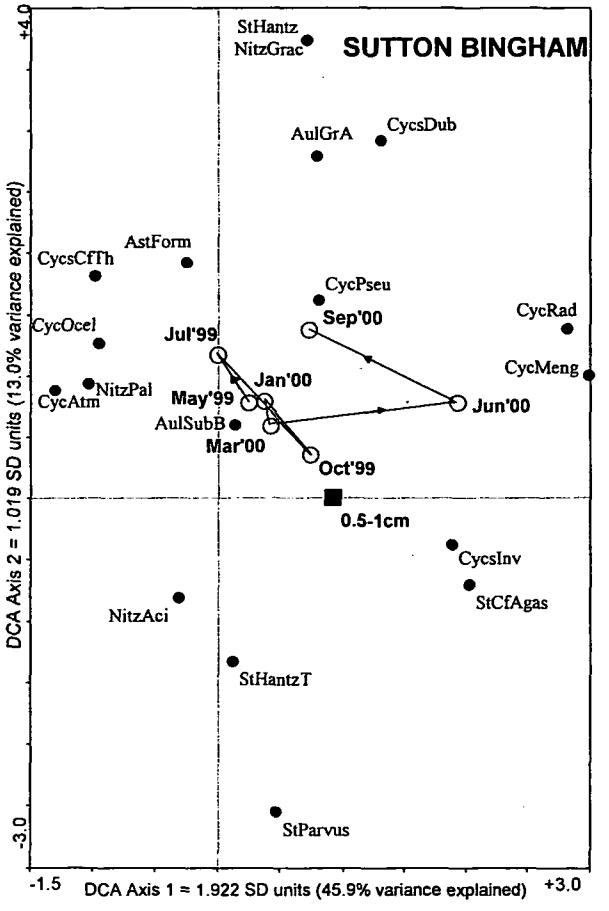


Figure 6.14 DCA ordination diagram illustrating Sutton Bingham's seven seasonal diatom plankton samples (active – open circles) and the 0.5-1 cm surface sediment planktonic diatom assemblage (passive – black square). For species codes see Appendix 3.

The 0.5-1 cm sediment sample is dominated by *A. subarctica* fo. *subborealis* (43%). However it is positioned to the right and below the central cluster of seasonal plankton samples due to the sub-dominance of *S.* cf. *agassizensis* (24%) and *S. parvus* (10%), taxa situated in the bottom half of the ordination diagram, and *C. radiosa* (7%), which is positioned to the right of the diagram.

6.2.8 Tittesworth

Figure 6.15 illustrates the seasonal data for Tittesworth reservoir. Algal populations appear to be closely correlated with water temperature. Temperature, Chla and diatom biovolumes follow a clear seasonal pattern, showing their highest values between May and October

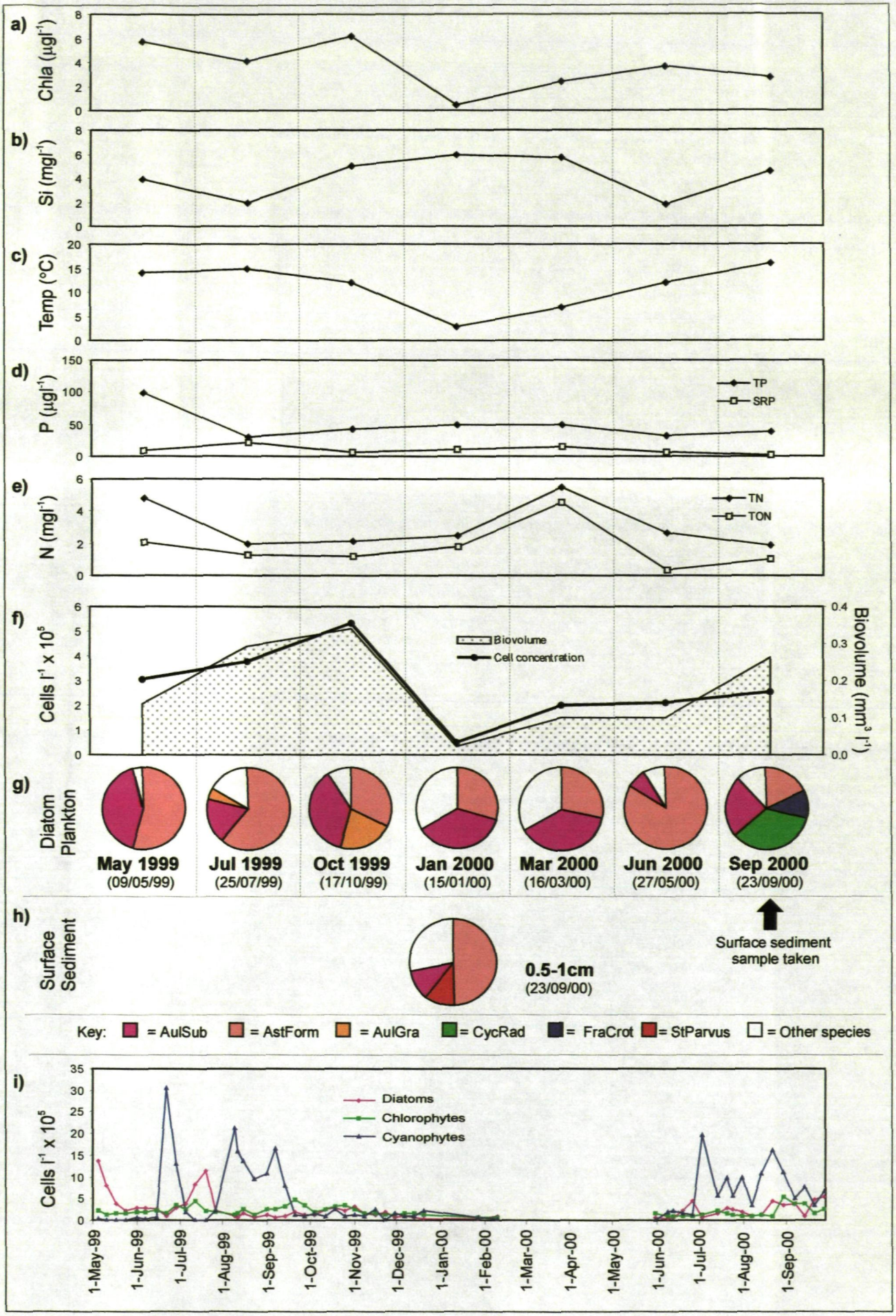


Figure 6.15 Tittesworth Reservoir; Seasonal data for key environmental variables (a-e), diatom cell concentrations and biovolumes (f), diatom plankton assemblages (g), surface sediment diatom assemblage (h), and algal concentrations (STW) (i).

1999, before decreasing markedly in January 2000 and then rising steadily between March and September 2000. TON and TN concentrations follow similar trends to those seen in other reservoirs in this study, with the highest concentrations recorded in March 2000. SRP concentrations remain consistently low throughout the sampling period; with the lowest concentrations generally following sustained algal blooms, particularly those comprising high cell concentrations of cyanophytes in the late summer and diatoms in the spring.

From late autumn to spring, Si concentrations are at their highest (~6 mgl^{-1}) and throughout this period *A. subarctica* dominates the diatom assemblage. It appears that the summer blooms of *A. subarctica* and *A. formosa* strip the water column of Si. Taxa such as *A. granulata* and *C. radiosa* bloom in the autumn when Si concentrations are recovering. Si does not appear to be limiting in Tittesworth and the seasonality of Si concentrations follow the inverse trend of both Temp and Chla.

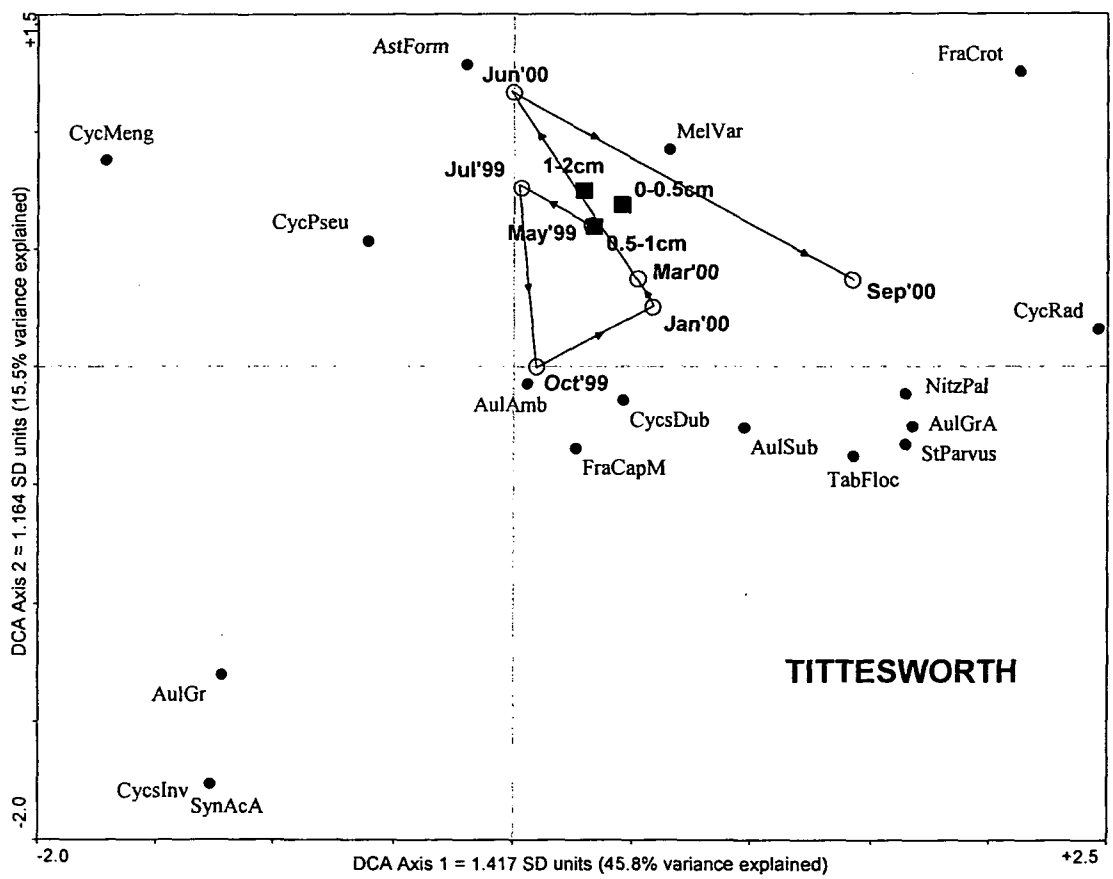


Figure 6.16 DCA ordination diagram illustrating Tittesworth reservoir's seven seasonal diatom plankton samples (active – open circles) and the 0-0.5 cm, 0.5-1 cm and 1-2 cm sediment planktonic diatom assemblages (passive – black squares). For species codes see Appendix 3.

According to Severn Trent Water's (STW) algal data, Tittesworth supports relatively low overall concentrations of algae in comparison to the other reservoirs discussed in this section. The summer to early autumn period of both 1999 and 2000 is dominated by cyanophytes. In July 1999, a bloom of diatoms immediately followed a decrease in cyanophytes. This is partially captured in the current study. Although according to STW data the time of sampling appears to have occurred at the end of the bloom, the chemical data appear to reflect conditions more favourable to cyanophytes, perhaps explaining why cyanophytes are subsequently able to regain dominance.

Figure 6.16 illustrates the trajectory followed by the seasonal diatom plankton assemblages in Tittesworth reservoir. Aside from September 2000, all seasonal plankton samples are dominated by differing percentage relative abundances of *A. subarctica* and *A. formosa* and are therefore positioned at different points between these two taxa. The October 1999 and July 1999 samples are pulled slightly away from this line due to the presence of *A. granulata* as a subdominant. The September 2000 sample is the only seasonal sample containing significant percentage relative abundances of *C. radiosa* (34%) and *F. crotonensis* (10%). This sample is located towards the right of the ordination plot where these taxa are situated. The 0-0.5 cm, 0.5-1 cm and 1-2 cm surface sediment samples are all located in relatively close proximity to one another. Being composed primarily of *A. formosa* and *A. subarctica*, the surface sediment samples lie between these two taxa. The occurrence of *C. radiosa* (only a small percentage relative abundance) in the 0-0.5 cm sediment sample pulls it slightly towards this taxon in ordination space.

6.2.9 Upper Tamar

Figure 6.17 displays the seasonal data for Upper Tamar reservoir. In common with the trends seen in most other reservoirs, Temp and Chla concentrations in Upper Tamar follow similar seasonal trajectories and Si concentrations track the inverse trend. SRP shows consistently low concentrations in Upper Tamar, generally <10 μgl^{-1}, thus P may be the limiting nutrient. It is not thought that Upper Tamar reservoir is N-limited since TON is generally in plentiful supply, perhaps due to the predominance of arable agriculture in the catchment.

Although diatoms and other algal groups generate relatively large seasonal blooms (up to ~120-140 cells l^{-1} $x10^5$), the contribution of cyanophytes is immense in terms of cell concentrations between June and late September 2000 (~1000-7000 cells l^{-1} $x10^5$).

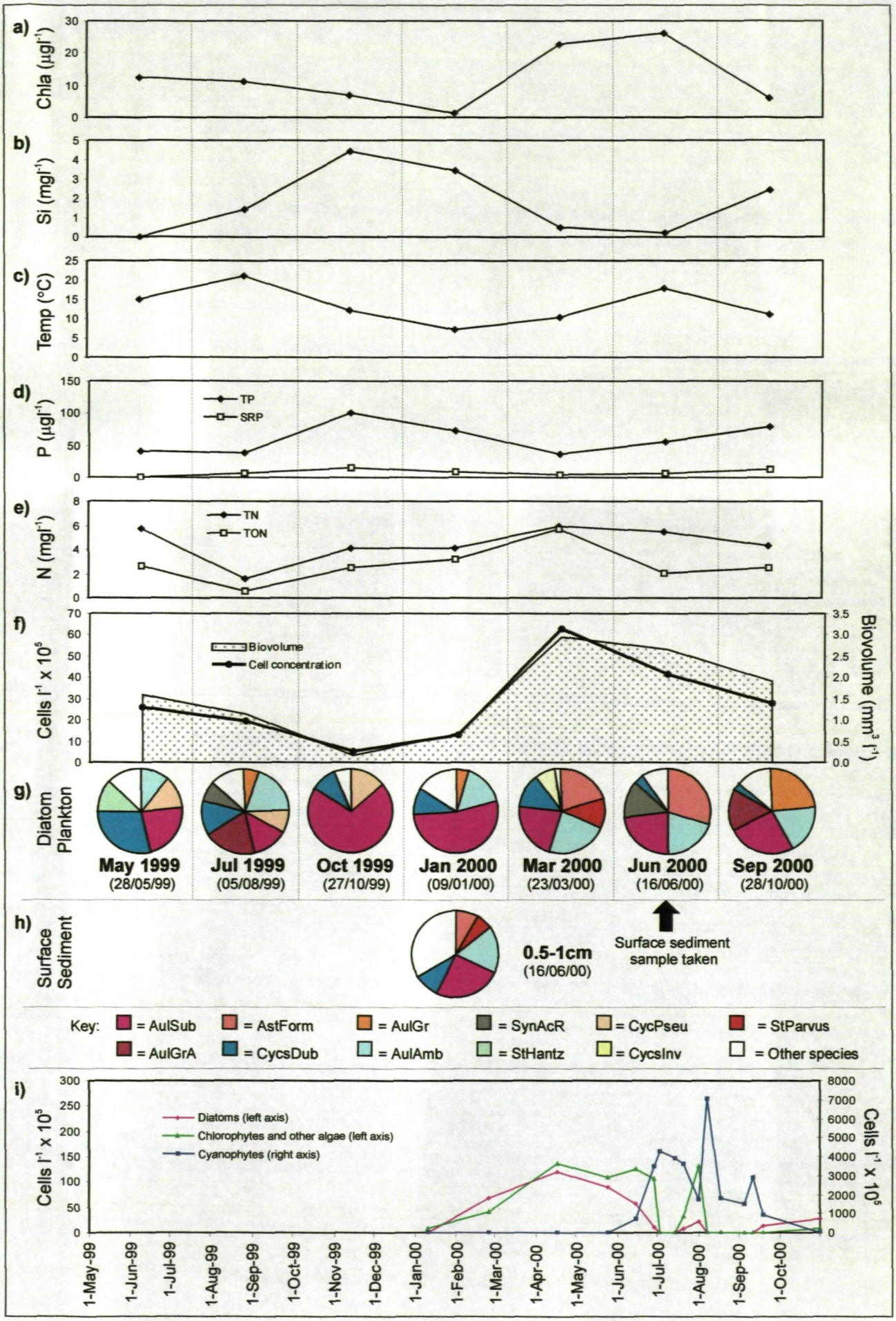


Figure 6.17 Upper Tamar Reservoir; Seasonal data for key environmental variables (a-e), diatom cell concentrations and biovolumes (f), diatom plankton assemblages (g), surface sediment diatom assemblage (h), and algal concentrations (SWW) (i).

The planktonic diatom assemblage at Upper Tamar is consistently diverse. No clear taxon seasonality is evident, unlike that seen in most other reservoirs. This may be because Upper Tamar is clearly dominated by cyanophytes, which reduce the growing season for other algae, thus leaving only short gaps between blooms for 'opportunist' diatoms to grow. According to South West Water (SWW), data the main diatom bloom occurs between February and June 2000, with diatom cell concentrations attaining a peak of ~120 cells l^{-1} $x10^5$ in April 2000. The current study's March and June 2000 samples partially record this bloom, although the April 2000 peak in cell concentrations is not captured since maximal diatom cell concentrations recorded in this study lie in the range 40 to 65 cells l^{-1} $x10^5$ only. The spring diatom bloom consists predominantly of *A. subarctica*, *A. ambigua* and *A. formosa*. The taxa *S. parvus*, *C. dubius* and to a lesser extent *C. invisitatus*, flank these populations in March 2000. In June 2000, *Synedra acus* var. *radians* is subdominant, with *C. dubius* and *C. invisitatus* still occurring but at low percentage relative abundance. *S. acus* var. *radians* only occurs during the summer months (July 1999 and June 2000). *A. granulata* and *A. granulata* var. *angustissima* occur predominantly during late summer and autumn.

Figure 6.18 illustrates the trajectory followed by the seasonal diatom plankton assemblages in Upper Tamar reservoir. Because the diatom plankton is consistently diverse, distances between seasonal samples are shorter than those seen in reservoirs where different single-species blooms prevail in successive seasons (e.g. Hollowell). The May 1999 sample is drawn slightly towards the bottom left-hand corner of the ordination plot through the combined influence of its dominant taxon *C. dubius* and its subdominants *Stephanodiscus hantzschii* and *C. pseudostelligera*. The July 1999 sample is very diverse, with seven taxa occurring at >5% relative abundance. This sample is therefore positioned centrally within the ordination space. The October 1999 and January 2000 samples are dominated by *A. subarctica* and are located relatively close to this taxon towards the top of the ordination space. The March 2000 and June 2000 samples are dominated by a combination of *A. subarctica*, *A. formosa* and *A. ambigua*; their location in ordination space lying between these taxa and determined by their relative proportions. In September 2000, *A. formosa* is replaced by *A. granulata* and *A. granulata* var. *angustissima*, thus positioning this sample centrally between *A. subarctica*, *A. ambigua*, *A. granulata* and *A. granulata* var. *angustissima*.

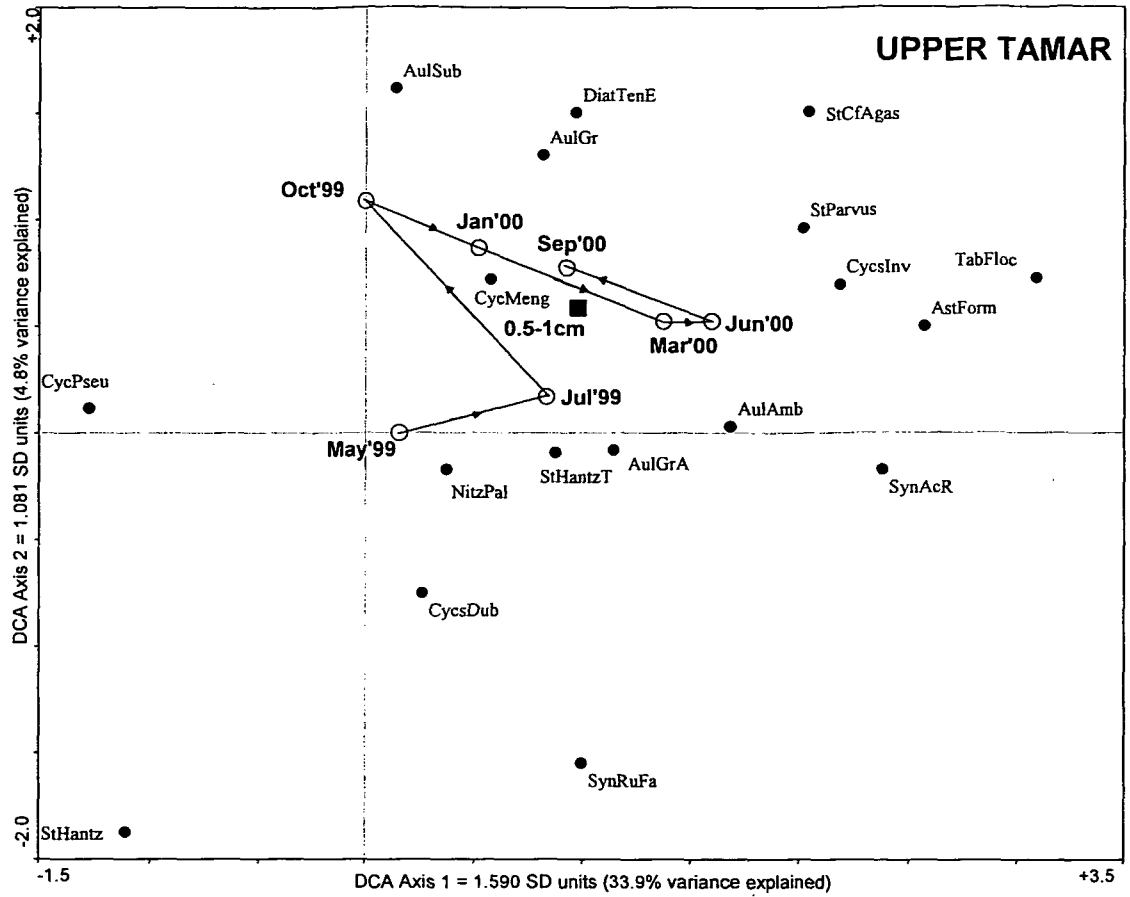


Figure 6.18 DCA ordination diagram illustrating Upper Tamar's seven seasonal diatom plankton samples (active – open circles) and the 0.5-1 cm surface sediment planktonic diatom assemblage (passive – black square). For species codes see Appendix 3.

The 0.5-1 cm sediment sample is located centrally in the ordination space, approximately mid-way between the January 2000 and March 2000 plankton samples, suggesting that it provides a good representation of the main diatom plankton bloom assemblage growing in the reservoir over the spring period prior to sediment sampling in June 2000. This is supported by the similarities shown between the spring 2000 plankton assemblages and the 0.5-1 cm sediment sample, the later of which consists of 30% *A. subarctica*, 21% *A. ambigua*, 12% *C. dubius*, 9% *A. formosa* and 8% *S. parvus*. Furthermore this suggests that Upper Tamar reservoir has a relatively rapid sedimentation rate.

6.2.10 Seasonality of planktonic diatom taxa – an overview

Examination of the temporal dynamics of planktonic diatom taxa in UK lowland reservoirs allows a better understanding of diatom ecology. Both in this study and in the literature, clear seasonality has been observed for many taxa (Lund, 1950, 1955, 1962; Reynolds, 1984a,b; Sayer & Roberts, 2001; Bradshaw & Anderson, 2002), whereas other species appear to have no seasonal growth preferences. The seasonal appearance, growth and

replacement of different diatom species are the result of competitive interactions, which are determined by the complex interactions and fluctuations in physical and chemical growth-regulating factors. It is informative to compare and contrast the reported trends from neolimnological phytoplankton research in natural lakes with those from artificial reservoir environments. The influence of artificial destratification on diatom plankton seasonality can be compared and contrasted with the patterns seen under conditions of natural thermal stratification and mixing.

Table 6.1 provides an overall summary of the seasonal preferences of selected planktonic diatom taxa. Taxon seasonality has been determined from seasonal plankton samples taken from the 9 reservoirs detailed in sections 6.2.1 to 6.2.9. In addition, seasonal plankton samples from numerous other calibration set sites have been analysed, the results of which have contributed further information on diatom species seasonality.

Taxon	Type	Spring	Summer (early)	Summer (late)	Autumn	Winter
Aulacoseira islandica	MC	•				
Diatoma vulgaris	P	•				
Stephanodiscus parvus	SC	•				
Aulacoseira granulata var. *angustissima*	SC	•	•	•		
Cyclotella pseudostelligera	SC	•	•	•		
Asterionella formosa	P	•	•		•	•
Fragilaria capucina var. *mesolepta*	P	•	•			•
Aulacoseira subarctica	SC	•	•		•	•
Aulacoseira subarctica fo. *subborealis*	SC	•	•		•	•
Aulacoseira ambigua	SC/MC	•	•	•	•	•
Cyclostephanos dubius	MC	•	•	•	•	
Cyclostephanos cf. *tholiformis*	SC	•	•	•	•	
Cyclotella atomus	SC		•	•		
Thalassiosira pseudonana	SC		•			
Cyclostephanos invisitatus	SC		•	•	•	
Cyclotella radiosa	MC		•	•	•	
Fragilaria crotonensis	P	•	•	•	•	
Cyclotella meneghiniana	MC/LC			•	•	
Actinocyclus normanii fo. *subsalsa*	LC			•	•	
Aulacoseira granulata	MC			•	•	
Stephanodiscus aff. *agassizensis*	MC			•	•	
Stephanodiscus neoastraea	LC			•	•	
Synedra acus (angustissima & radians)	P			•	•	
Tabellaria flocculosa	P			•	•	
Nitzschia fonticola	P				•	
Nitzschia palea	P				•	

Table 6.1 **Seasonality of planktonic diatom taxa (from examination of seasonal plankton samples), ordered in terms of seasonal preference, from spring to winter. 'Type' refers to diatom taxon form – P = pennate, LC = large centric, MC = medium centric, SC = small centric.**

Two main periods of diatom growth are usually observed and described in the literature: the spring and autumn blooms (Reynolds, 1984b; Willén, 1991). In this study, the main periods of diatom growth agree to some extent with these observations. However the presence and persistence of diatoms in terms of cell concentrations / biovolumes often occur throughout the year, also demonstrating shifts in species composition from season to season. Further, the patterns observed in different reservoirs are highly variable, with different sites presenting differing environmental conditions and in turn supporting diatom populations of varying composition and displaying contrasting seasonalities.

In this study, taxa typically seen blooming during the vernal period include *Aulacoseira islandica*, *Diatoma vulgaris*, *S. parvus*, *A. granulata* var. *angustissima* and *A. formosa*. In the literature, these taxa are often described as showing a preference towards cool, clear, nutrient-rich conditions. For example, in Lake Windermere *A. formosa* in combination with *A. subarctica*, and in more recent years *A. islandica*, consistently co-dominate the spring bloom (Reynolds & Irish, 2000). These authors relate the ability of these taxa to be "first in the field" to the provision of sufficiently large inocula and upon their more efficient light harvesting ability. The renewal of available nutrient and silica stocks over the winter period also enables the resource requirements of these taxa to be satisfied. Consequently, Lund (1950) showed that exhaustion of silica was usually responsible for the termination of the spring diatom bloom in Windermere.

Taxa showing a preference for growth during the summer and autumn periods include *C. radiosa*, *F. crotonensis*, *C. dubius*, *C. invisitatus*, *A. normanii* fo. *subsalsa*, *A. granulata*, *S. neoastraea*, *S. acus*, *T. flocculosa*, *F. capucina* var. *mesolepta*, *Nitzschia fonticola* and *Nitzschia palea*. The preference of these taxa for the late summer period suggests that all are capable of sustaining growth under warmer conditions, often at lower concentrations of nutrients and dissolved silica than in spring and when competition for resources from other algal groups is high. In common with results presented by Bradshaw & Anderson (2002), *C. dubius* occurred predominantly during the late summer and autumn period, but was also an important component of the spring bloom in some reservoirs, as was found by Sayer & Roberts (2001). It was noted in this study however that the cell size of *C. dubius* in the spring was generally smaller than that recorded in the late summer and autumn, perhaps indicating that this taxon is capable of growth following depletion of the water column of both nutrients and silica by taxa blooming earlier in the spring. To compensate for reduced resource availability, spring cell sizes are comparatively small compared with those seen in the late summer and autumn period when silica is more plentiful following diatom

dissolution and release of silica from the sediments by diffusion and bioturbation (Lampert & Sommer, 1997).

A. granulata and *F. crotonensis* are typically found in greatest abundance in the warmer waters of the late summer and autumn plankton assemblages, suggesting they are capable of efficiently harvesting light under warm-water conditions and plentiful nutrient concentrations. Reynolds *et al.* (1983) reported that the growth dynamics of *F. crotonensis* may be satisfied at higher light levels, thus explaining its tendency to flourish in summer. Both *A. granulata* and *F. crotonensis* are also often described as requiring sufficient water turbulence to enable their rapidly sinking cells to remains within the photic zone (Reynolds, 1984b; Bailey-Watts, 1986; Gómez et al., 1995; Tibby, 2004). In many reservoirs, this turbulence is provided by artificial destratification, where in natural lakes the breakdown of thermal destratification brought about by an increase in stormy conditions provides the necessary movement of the water column.

Although there are broad intra-annual trends in the seasonality shown by individual diatom taxa, many species exhibit inter-annual variations in their seasonal growth patterns. The interplay between inoculum size and growth efficiency is described by Reynolds & Irish (2000) as providing "scope for considerable inter-annual variability in the composition and abundance of the phytoplankton, which is amplified by year-to-year differences in weather conditions" (p.24). These effects are compounded by the intervention of dynamic biological factors such as grazing by zooplankton and fungal epidemics (Canter-Lund & Lund, 1995).

Diatoms are typically *r*-selected phytoplankton taxa, capable of rapidly expanding their populations when appropriate conditions prevail. Thus, in natural lakes, diatoms tend to dominate phytoplankton assemblages during cool, mixed periods in the spring and autumn (Reynolds, 1984b; Reynolds & Irish, 2000). *K*-strategists such as cyanophytes are more prevalent during periods of water column stability, where their more efficient use of available resources enables them to establish large, stable populations more tolerant of environmental stresses than the r-strategists. However, in artificially destratified reservoirs, the effect of destratification can result in longer periods of mixing, which in turn influences phytoplankton periodicity, increasing the scope for opportunist *r*-strategists to dominate (Reynolds, 1999). For example, in the current study *A. formosa*, which is typically reported to favour the vernal period (e.g. Lund, 1950; Round, 1971), is encountered in all seasons in the plankton of destratified Tittesworth reservoir. Reynolds *et al.* (1983, 1984) observed that artificial mixing in limnetic enclosures resulted in the renewed net growth of *A. formosa*,

but that re-stratification led to the elimination of diatoms, in favour of *K*-selected phytoplankton groups. Thus in reservoirs there appears to be a tendency for artificial destratification to break down the defined seasonal species trends commonly seen in deep natural lakes. Similarly, reservoirs that do not have artificial destratification but are shallow (e.g. Upper Tamar) are also observed to support this pattern. The relatively shallow nature of this waterbody leads to an increase in the influence of wind-mixing and in turn the release of growth resources from the sediments. This may explain why *C. dubius*, *A. subarctica* and *A. ambigua* do not show defined seasonal patterns of growth in Upper Tamar reservoir.

6.3 Similarities and dissimilarities between seasonal diatom plankton assemblages in the nine reservoirs (DCAs)

DCA ordination techniques were employed to determine the similarities and dissimilarities between the seasonal planktonic diatom assemblages and trajectories between these assemblages across the nine reservoirs. The DCA was performed on 39 planktonic diatom species (life form determined from habitat samples examined in the current study and from a review of the literature) and 63 samples (seven seasonal samples from each of the nine reservoirs).

The results from this analysis are presented in Table 6.2 and show that the first two axes of the DCA account for only 12.3% and 8.8% respectively of the variation in the diatom species data. These values are typical of noisy, species-rich datasets (Jongman *et al.*, 1995) and are comparable in magnitude to the results presented for the UK lowland reservoirs calibration set in the previous chapter. Community variation, as indicated by the lengths of the species gradients (5.050 and 5.558 standard deviation units respectively), spans a large range, indicating that most species responses are best approximated by unimodal response models (Jongman *et al.*, 1995), thus supporting the utilisation of CCA for direct gradient analysis in section 6.4.

Axis	Eigenvalue	Length of gradient (SD units)	Cumulative variance represented (%)
1	0.830	5.050	12.3
2	0.601	5.558	21.1 (8.8)
3	0.431	3.409	27.5 (6.4)
4	0.274	2.348	31.6 (4.1)

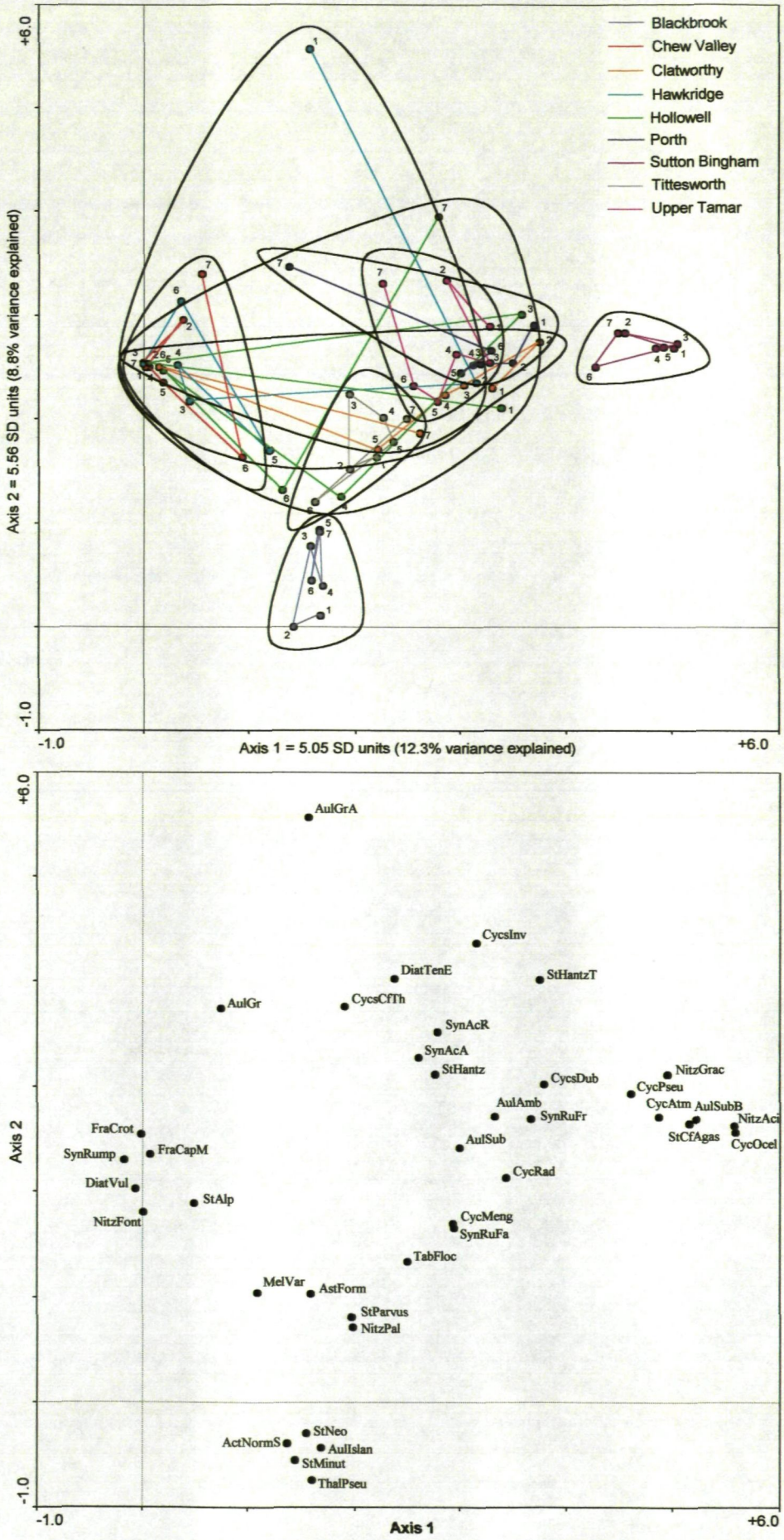
Table 6.2 Results of DCA analysis for 39 planktonic diatom taxa and 63 samples. Numbers in parentheses are individual axes contributions.

Figure 6.19 shows the change in species composition over time (May 1999 to October 2000) and illustrates differences and similarities between the seasonal planktonic diatom assemblages of the nine reservoirs. For each reservoir, the species composition of individual seasonal samples is plotted as a single point in ordination space. The numbers 1 to 7 indicate the individual seasonal samples for each site. Table 6.3 shows the seasonal sample to which each number corresponds. The seven seasonal samples for individual reservoirs are then connected with vectors so that time trajectories illustrating relative changes in species composition can be seen.

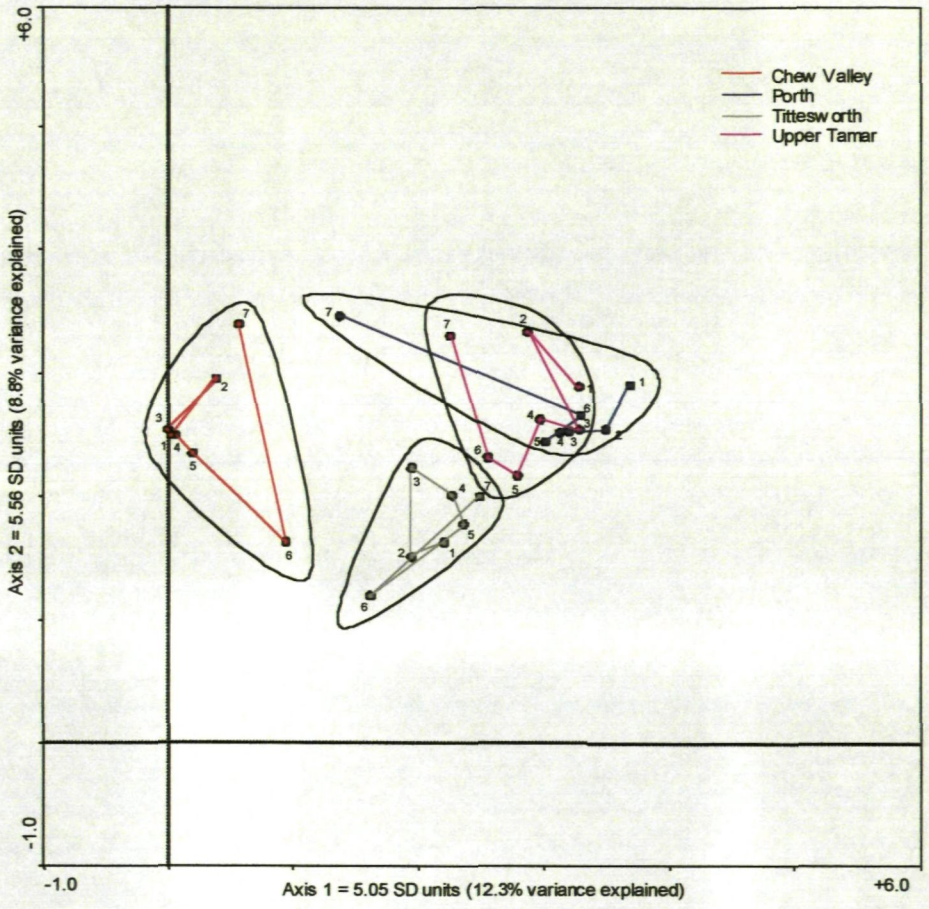
Season number	1	2	3	4	5	6	7
Seasonal sample	May 1999	July 1999	October 1999	January 2000	March 2000	June 2000	September 2000

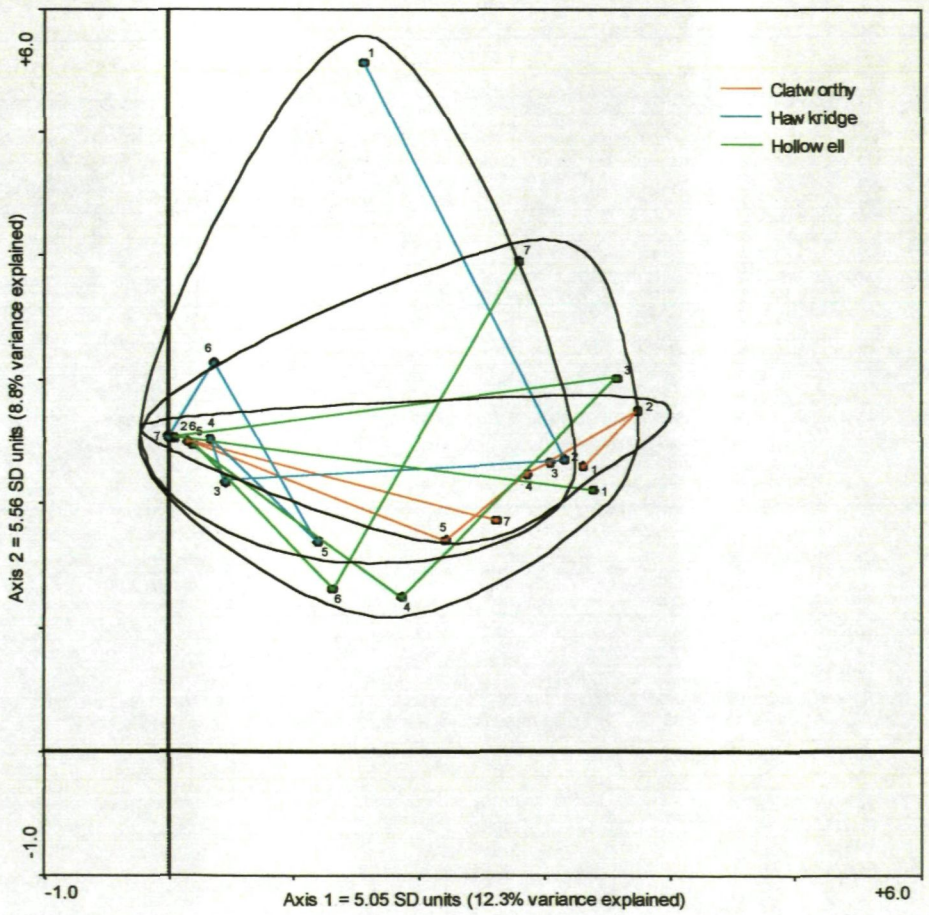
Table 6.3 The seasonal samples to which each season number in Figure 6.19 corresponds.

All sites experience a wax and wane of different diatom species on a seasonal basis, with some sites demonstrating a less pronounced shift in species assemblages than others. It is recognised that the ordination of taxa and hence seasonal samples is largely dependent upon the sites chosen for inclusion in the ordination. For example, Sutton Bingham and Blackbrook are the most dissimilar, both from each other and from the other seven reservoirs in terms of their seasonal planktonic diatom species composition. The species found in Sutton Bingham's plankton are consistently different to those found in the other sites (e.g. *A. subarctica* fo. *subborealis* and *Stephanodiscus* cf. *agassizensis*), illustrated by the isolated position of this reservoir towards the right-hand side of the ordination diagram (Figure 6.19a & b). Blackbrook also supports many taxa that are absent from the plankton of the other reservoirs (e.g. *A. normanii* fo. *subsalsa*, *S. neoastraea*, *A. islandica* and *T. pseudonana*), positioning this site towards the bottom of the ordination plot (Figure 6.19a & b). If the seasonal plankton samples from a greater number of reservoirs had been examined and subsequently included in the DCA analysis, then increased overlap might have been seen and the seasonal plankton samples from Blackbrook and Sutton Bingham may not have appeared as distinctive isolated clusters.



Figures 6.19a & b **DCAs illustrating the seasonal diatom assemblage trajectories for nine selected reservoirs; a) samples, b) species. Hulls delineate sites.**





Figures 6.19c & d **Detail of Figure 6.19a showing selected sites; c) Chew Valley, Tittesworth, Upper Tamar and Porth, d) Hawkridge, Hollowell and Clatworthy. Hulls delineate sites.**

Porth and Upper Tamar share a number of species in common (e.g. *A. subarctica*) and exhibit some similarities in the seasonality of their diatom plankton assemblages, as illustrated by the proximity of their corresponding seasonal samples. The overall trajectories for these sites are located in close proximity and towards the right-hand side of the DCA ordination diagram (Figure 6.19a & c). Tittesworth's seasonal trajectory spans a relatively small area and is located towards the bottom of the ordination space. Chew Valley's trajectory is of moderate size and is confined to the left-hand side of the ordination space (Figure 6.19a & c).

Clatworthy, Hawkridge and Hollowell have trajectories spanning large areas of the ordination space (Figure 6.19a & d). The trajectories of these three sites encompass the three distinct sectors of the ordination space, associated with Upper Tamar/Porth, Tittesworth and Chew Valley. Seasonal diatom plankton assemblages for Clatworthy, Hawkridge and Hollowell move between and link these three sectors. Whilst it is not possible, based on the data from only three sites, to draw any firm conclusions from the movements of the trajectories, it appears that the plankton assemblages of these three sites may move cyclically between the three separate sectors. Most notable are the locations of winter and spring samples in close proximity to Tittesworth's sector (Hollowell - January 2000; Hawkridge and Clatworthy - March 2000). The trajectories then move between Chew Valley's sector and onto that of Upper Tamar/Porth over the summer and autumn period. The June 2000 samples from Clatworthy and Hawkridge are ordinated in the Chew Valley sector, whilst the July 1999 samples from Clatworthy and Hawkridge, and the October 1999 samples from Clatworthy and Hollowell are ordinated in the Porth/Upper Tamar sector. This apparent shift between the three distinct sectors may be of relevance in demonstrating a cyclical seasonal trend.

The distribution of species in ordination space (Figure 6.19b) drives the cyclicity described above. No taxa are positioned in the centre of the ordination diagram. This reflects both the distinction in diatom species assemblages between groups of sites and seasons. Cyclicity is highlighted in the ordination of taxa such as *F. crotonensis* and *A. granulata* (late summer / autumn species) against the spring blooming taxa *S. parvus*, *A. subarctica* and *A. formosa*. However, there appears to be an absence of planktonic diatom taxa completing the cyclical pattern towards the top left-hand region of the ordination space. *A. granulata* occurs alone in this area, providing a link between the Chew Valley and Porth/Upper Tamar sectors. However the importance of this observation may be limited, since the position of *A. granulata* in ordination space is dependent upon the tolerance ranges of other species

included in the ordination. In autumn 2000 Upper Tamar and Porth reservoirs supported diatom populations composed of varying proportions of *A. granulata*. The presence of a moderate (Upper Tamar) to high (Porth) percentage relative abundance of *A. granulata* in these autumn 2000 plankton samples brings their trajectories within close proximity of Chew Valley's *A. granulata*-dominated autumn 2000 plankton assemblage.

These broad conclusions are based on the data from only a small number of sites. It may be informative to include seasonal plankton data from a greater number and diversity of sites, perhaps enabling clearer patterns to emerge. The ordinations of some taxa are influenced by their occurrence in the seasonal plankton samples of only one site. For example *T. flocculosa* only occurs at relatively low abundance in the plankton of Tittesworth reservoir, thus its position on the ordination diagram is highly dependent upon the pull of other taxa occurring in the same seasonal sample. The inclusion of further sites supporting *T. flocculosa* in their seasonal plankton should lead to an improvement in the ordination of this taxon and hence improved definition of the cyclical patterns.

6.4 Relationships between seasonal diatom plankton assemblages and environmental variables (CCAs).

CCA was used to explore relationships between seasonal diatom plankton assemblages and a corresponding suite of measured environmental variables. CCA was carried out with 39 active planktonic diatom taxa and 63 active samples; the same as those used for the DCA carried out in section 6.3. The associated suite of environmental data consisted of seasonal measurements for 10 variables. These were Chlorophyll-*a* (Chla), secchi depth (SD), silica (Si), total phosphorus (TP), total nitrogen (TN), Si:TP ratio, TN:TP ratio, pH, conductivity (EC) and temperature (Temp). Summary statistics for these 10 variables are displayed in Table 6.4. Although the biologically available forms of N and P, total oxidised nitrogen (TON) and soluble reactive phosphorus (SRP), were originally considered for inclusion in the analysis, their concentrations were highly inter-correlated with concentrations of TN and TP, indicating that TN and TP could adequately express nutrient concentrations in the CCA. In addition, constrained CCAs showed that TON and SRP explained less independent variation in the species data than TN and TP, further indicating their redundancy in the analysis. TN:TP and Si:TP were included in the suite of variables because the ratios between environmental variables often change dramatically on a seasonal basis and can influence the competitive abilities of different diatom taxa and algal groups (Kilham, 1971; Tilman, 1976, 1977; Kilham & Tilman, 1979; Tilman *et al.*, 1982; Kilham, 1984, 1986; Barica, 1990; Interlandi *et al.*, 1999; Smith & Bennett, 1999; Guildford & Hecky, 2000).

Environmental variable	Acronym	Units	Samples	Mean	Median	Min	Max	St.Dev
Water temperature	Temp	°C	63	13.59	13.00	3.00	24.00	4.82
pH (pH)	pH	pH	63	7.82	7.83	6.71	9.36	0.58
Conductivity (EC)	EC	μScm^{-1}	63	314.89	356.00	114.00	502.00	121.53
SiO_2-Si	Si	mgl^{-1}	63	2.56	2.01	0.00	7.58	2.02
TN	TN	mgl^{-1}	63	3.87	3.36	0.84	14.42	2.38
TP	TP	μgl^{-1}	63	69.62	50.00	9.00	445.00	74.79
Chlorophyll-*a* (mean)	Chla	μgl^{-1}	63	7.86	4.80	0.10	34.60	7.89
Secchi depth	SD	cm	63	210.71	190.00	50.00	500.00	120.30
Si:TP ratio	Si:TP	-	63	63.35	42.81	0.00	398.00	72.86
TN:TP ratio	TN:TP	-	63	117.00	68.70	2.10	1101.00	163.10

Table 6.4 Summary statistics for the 10 environmental variables measured over 7 seasons in 9 reservoirs.

An attempt was made to normalise the environmental variables using either $\log_{10}$ or square root transformations before their incorporation into the CCA. The choice of transformation for each variable is displayed in Table 6.5. EC and TN:TP did not transform to normal distributions using the above data transformations, however the data most closely resembling a normal distribution were selected for inclusion in subsequent direct gradient analyses. Examination of the variance inflation factors (VIFs) for each of the 10 environmental variables showed that all were <7, indicating minimal inter-correlation between the 10 variables and supporting their inclusion in the CCA.

Variable	Before transformation: (P value)	Normally distributed?	After **Log_{10}** transformation: (P value)	Normally distributed?	After **Sq root** transformation: (P value)	Normally distributed?
Temp	0.546	Yes	N/A	N/A	N/A	N/A
pH	0.531	Yes	N/A	N/A	N/A	N/A
EC	0.000	No	0.000	No	0.000	No
Si	0.000	No	0.001	No	0.178	Yes
TN	0.001	No	0.886	Yes	N/A	N/A
TP	0.000	No	0.628	Yes	N/A	N/A
Chla	0.000	No	0.077	Yes	N/A	N/A
SD	0.000	No	0.236	Yes	N/A	N/A
Si:TP	0.000	No	0.014	No	0.412	Yes
TN:TP	0.000	No	0.015	No	0.000	No

Table 6.5 Data transformations required for the 10 environmental variables (shaded boxes indicate transformations required to achieve normal distributions for each variable. Where normalisation was not achieved, shaded boxes indicate the data chosen for use in the subsequent CCA).

Results from the CCA ordination, run with 39 active species, 63 active samples and 10 active environmental variables can be seen in Table 6.6. Axis 1 explains the majority of variation in both the species and species/environment data (7.7% and 29.4% respectively) and shows the highest correlation between species and environment (0.835). However a large proportion of variation is also captured by axis 2 (5.6% and 21.8% in the species and

species/environment data respectively). This was unsurprising since the 9 reservoirs included in the seasonality study were to some extent selected on the basis of differences in their seasonal diatom assemblages and environmental characteristics.

Axis	Eigenvalue	Species / environment correlation	Cumulative % variance (species)	Cumulative % variance (species / environment)	Sum of all unconstrained eigenvalues	Sum of all canonical eigenvalues
1	0.518	0.835	7.7	29.4		
2	0.383	0.779	13.3 (5.6)	51.2 (21.8)		
3	0.269	0.712	17.3 (4.0)	66.6 (15.4)		
4	0.219	0.611	20.5 (3.2)	79.0 (12.4)		
					6.767	1.759

Table 6.6 Results of CCA on the 39 diatom species with 63 active samples and 10 environmental variables (numbers in parentheses are individual axes contributions).

The most important environmental variables in determining the seasonality of diatom assemblages in the 9 sites were SD, Si, EC and pH. A series of constrained CCAs (results not presented) showed that these were the only environmental variables that could explain significant independent variation in the seasonal diatom plankton data. TP, TN, Temp, Si:TP, TN:TP and Chla were of secondary importance, unable to explain significant independent variation. These results indicate that the variables of greatest importance in determining seasonality in diatom assemblages are similar to those able to explain the majority of variance in the surface sediment diatom assemblages in the UK lowland reservoir calibration set (see previous chapter). This is to be expected because the seasonal diatom plankton assemblages in individual reservoirs should directly determine the fossil assemblages constituting the surface sediment samples. Aside from this overall similarity, Si concentrations and the Si:TP ratio are more important in explaining seasonal variations in species assemblages than in determining the resultant fossil assemblages (see previous chapter). This is probably because the fossil assemblages dampen down the seasonal influence on diatom populations of changing water chemistry. Temperature was expected to be of significance in explaining variations in seasonal diatom plankton assemblages according to published observations for natural lakes e.g. Reynolds & Irish (2000). This suggests that other factors, for example Si concentrations and light availability, may be of overriding importance in explaining diatom plankton seasonality in artificial reservoirs.

Despite SD, Si, EC and pH being of greatest overall importance in explaining seasonal variations in CCA analyses, other factors such as turbulence, which were not measured in

the current study, are known to be important in determining seasonal diatom species assemblages (Reynolds, 1984b). Naselli-Flores (2000) reported that the ratio of mixing to euphotic depth i.e. turbulence, was an important factor in determining seasonal phytoplankton assemblages in Sicilian reservoirs.

Figures 6.20a & 6.20b display the CCA ordination diagrams illustrating the seasonal trajectories of the planktonic diatom species assemblages in the 9 reservoirs in relation to the 10 seasonally measured environmental variables. The differences in environmental characteristics between the 9 sites appear to have a greater influence on the ordination of samples than the influence of individual species. For example, the June 2000 diatom plankton assemblage in Clatworthy is dominated by *F. crotonensis*. The ordination of this sample in the DCA placed it in almost the same position as those samples from October 1999 and January 2000 dominated by *F. crotonensis* from Chew Valley reservoir (see Figure 6.19a/b). However in the CCA (Figure 6.20a/b), the differences in the environmental characteristics (particularly in terms of EC and pH) of Chew Valley and Clatworthy reservoirs leads to these similarly composed samples being disparately located in ordination space.

As mentioned above, Clatworthy is reasonably distinct both in terms of its environmental characteristics and diatom assemblages. It is the only site supporting *T. flocculosa* and *S. rumpens* var. *familiaris*, a reflection of its comparatively low EC and pH conditions, and low concentrations of TP. Tittesworth shares some environmental characteristics with Clatworthy, including low to moderate EC and pH conditions and generally low water temperatures, reflecting the upland nature of these sites.

Blackbrook and Hollowell, and to some extent Hawkridge, display similar diatom assemblages and display approximately average water chemistry characteristics. Their seasonal diatom plankton assemblages are dominated by *A. formosa* during the winter/spring period, as evinced by the relatively close proximity of the seasonal plankton samples 4 and 5 in Figure 6.20a.

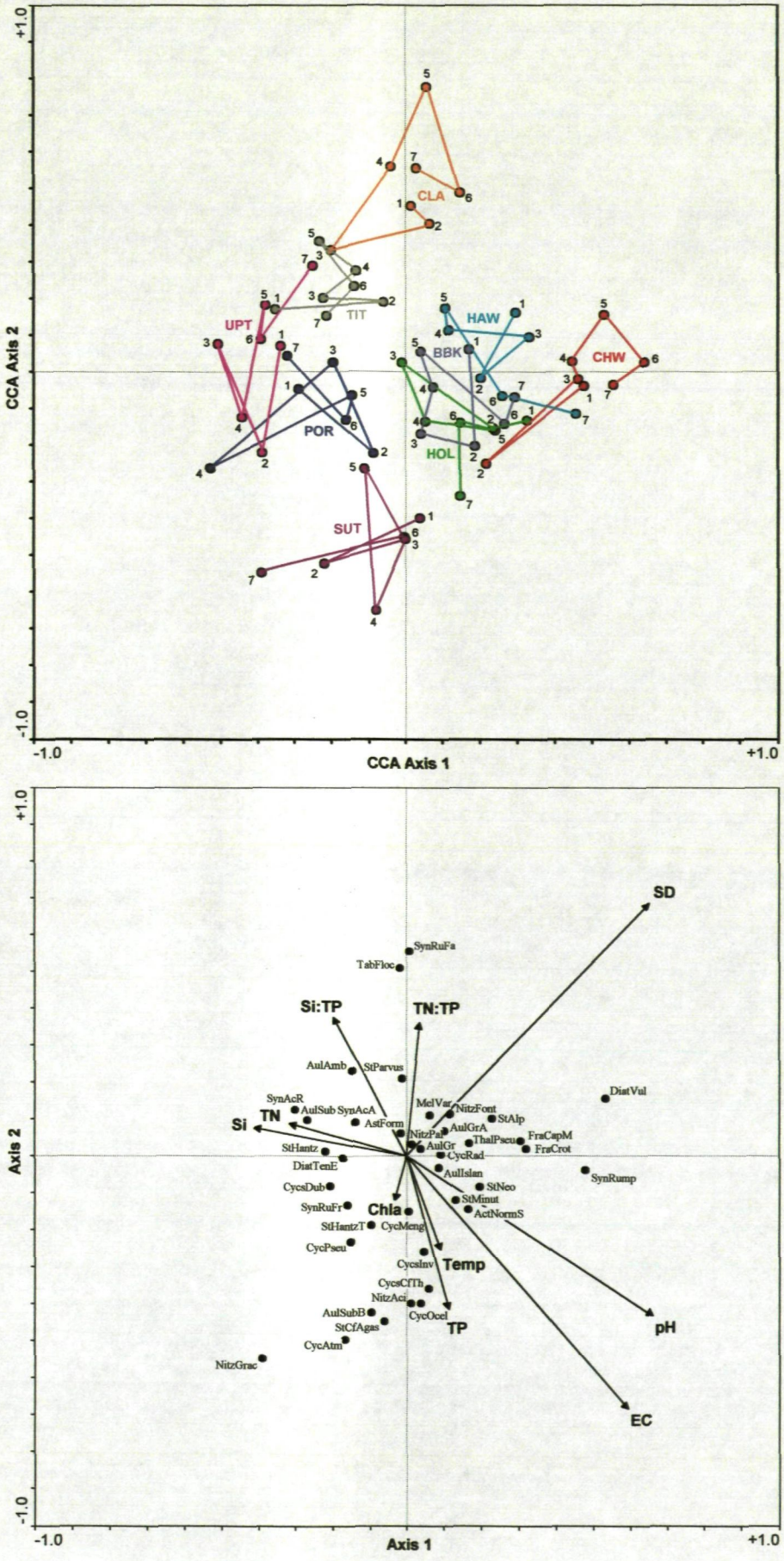


Figure 6.20a and b **CCA ordination diagrams illustrating the seasonal trajectories in the plankton of nine selected reservoirs; a) samples and seasonal trajectories, b) species and environmental variables.**

Sutton Bingham can be considered the most distinct of the nine sites both in terms of its diatom assemblage and its environmental characteristics. This is largely because its assemblage comprises a high relative abundance of taxa not seen (e.g. *A. subarctica* fo. *subborealis* and *S.* cf. *agassizensis*) or occurring at a lower relative abundance (e.g. *C. pseudostelligera*) in the other sites. In addition, Sutton Bingham is a relatively shallow site, with low water clarity, and high Chla and TP concentrations.

Upper Tamar and Porth reservoirs share similar environmental and species characteristics. Both sites have moderately high Si and TN concentrations although the relatively shallow nature of these sites reduces the water clarity and increases Chla concentrations.

The ordination of taxa in Figure 6.20b suggests that *T. flocculosa*, *S. rumpens* var. *familiaris*, *Synedra acus* var. *radians*, *Synedra acus* var. *angustissima*, *A. ambigua*, *S. parvus*, *A. subarctica* and *A. formosa* are all taxa that require cooler water conditions, moderate to high Si concentrations and are most competitive under conditions of low TN:TP ratios.

6.5 Differences in seasonal diatom assemblages

Ordination space distances were measured (in standard deviation units) between successive seasonal diatom plankton samples in each of the 9 reservoirs. These distances were measured and analysed to determine the extent and statistical significance of variations, both within and between sites, in terms of seasonal species assemblages. Table 6.7 presents the measurement data, which has been drawn from Figures 6.19a.

The winter period October 1999 – March 2000 covers the shortest overall distance in DCA ordination space (October 1999 – January 2000 = 0.49 units; January 2000 – March 2000 = 0.63 units). This may reflect the comparatively static diatom community structure present in the nine selected reservoirs over this period, which in turn probably reflects lower algal productivity. During times of lower productivity, plankton assemblages might be expected to comprise remnants of diatom blooms that occurred earlier in the year, hence the lesser extent of change. In addition, increased wind-induced turbulence at this time may entrain into the water column recently sedimented diatom frustules. Since the seasonal plankton samples were examined after the removal of their cell contents, the extent to which 'dead' frustules have been incorporated into the seasonal plankton assemblages has not been assessed.

Site	Distance covered in each seasonal period (standard deviation units)						Total	Mean	Rank
	1 May'99-Jul'99	2 Jul'99-Oct'99	3 Oct'99-Jan'00	4 Jan'00-Mar'00	5 Mar'00-Jun'00	6 Jun'00-Sep'00			
Blackbrook	0.26	0.76	0.38	0.53	0.50	0.47	2.91	0.49	2
Chew Valley	0.56	0.56	0.06	0.21	0.74	1.76	3.88	0.65	6
Clatworthy	0.62	0.79	0.21	0.82	2.18	2.53	7.15	1.19	7
Hawkridge	3.53	2.68	0.35	1.18	1.62	0.68	10.03	1.67	8
Hollowell	3.03	3.53	2.41	2.06	1.59	2.97	15.59	2.60	9
Porth	0.41	0.29	0.06	0.15	0.35	2.06	3.32	0.55	3
Sutton Bingham	0.47	0.47	0.24	0.06	0.65	0.41	2.29	0.38	1
Tittesworth	0.29	0.71	0.38	0.24	0.94	1.18	3.74	0.62	5
Upper Tamar	0.59	0.88	0.35	0.47	0.26	1.00	3.56	0.59	4
Total	9.76	10.68	4.44	5.71	8.82	13.06	52.47		
Mean	1.08	1.19	0.49	0.63	0.98	1.45			
Median	0.56	0.76	0.35	0.47	0.74	1.18			
Standard deviation	1.26	1.12	0.73	0.64	0.66	0.93			
Rank	4	5	1	2	3	6			

Table 6.7 Distance in ordination space between the planktonic diatom assemblages recorded in the phytoplankton in different seasons at 9 selected reservoirs. Sites are ranked from 1 (shortest distance) to 6 (longest distance).

The summer to autumn period (May 1999 – October 1999 and June 2000 – September 2000) sees the largest changes in diatom assemblages, reflecting the shifts in community structure during the main plant growth season. Changes in the diatom community structure throughout this period result from a combination of differing environmental preferences and competition for resources from other algal groups, particularly chlorophytes and cyanophytes. A further possibility is that, whereas there are few diatom taxa adapted to growth during the early spring period, a greater diversity of taxa may be able to grow in the summer period because ambient environmental conditions are similarly diverse and less predictable.

The degree of difference in ordination space distance between successive seasonal planktonic diatom assemblages was statistically assessed using the Kruskal-Wallis non-parametric test. The results of this test showed that overall, the differences between seasons were significant at the 95% confidence level ($P = 0.041$). However, when Mann-Whitney non-parametric tests were performed on the distances between individual seasonal periods, results indicated that statistically significant differences existed only between some pairs of seasonal samples and that these significant results were driving the overall significant result of the Kruskal-Wallis test. Table 6.8 displays the results of the Mann-Whitney tests, where statistically significant differences (at the 95% confidence level) between seasonal periods are highlighted. Results indicate that there are only statistically significant differences

between seasonal periods 3 and 1, 3 and 2, 3 and 5, 3 and 6, and 4 and 6 (for periods see Table 6.7). The change in diatom plankton assemblage composition over seasonal period 6 (June 2000 to September 2000) is considerably greater than that seen in seasonal periods 3 (October 1999 to January 2000) and 4 (January 2000 to March 2000). The change in period 3 (October 1999 to January 2000) is less than that seen in periods 1 (May 1999 to July 1999), 2 (July 1999 to October 1999), 5 (March 2000 to June 2000). These results support the observations discussed above in relation to the changes in diatom plankton community structure in different seasons.

Seasonal period	Seasonal period 1	2	3	4	5
2	0.288	-	-	-	-
3	0.027	0.010	-	-	-
4	0.301	0.145	0.480	-	-
5	0.508	0.860	0.034	0.158	-
6	0.216	0.508	0.004	0.047	0.251

Table 6.8 **Results of Mann-Whitney statistical tests determining statistical differences between seasonal diatom plankton assemblages. Statistically significant differences ($P < 0.05$) are shaded (for season periods see Table 6.8).**

6.6 Taphonomy and its implications

It is useful to consider taphonomy, i.e. the differences between live and fossil assemblages, since its implications are of fundamental importance in palaeolimnological studies. Taphonomic processes, such as grazing, dissolution and breakage, affect the transition from live to fossil diatom assemblages and thus affect the accuracy of interpretations drawn from sedimentary records. Therefore in this section the differences between mean 'live' seasonal diatom plankton assemblages and those laid down in the sediment record are explored.

M1, M2, M3 and M4 are codes for the different time periods over which 'mean' diatom plankton assemblages have been determined. Table 6.9 displays the seasonal plankton samples that have been used to calculate the 'mean' diatom plankton assemblage for each period M1 to M4. Means M1, M2 and M3 are described as spanning 12-month periods since each mean comprises four seasonal samples, considered together to represent annual phytoplankton cycles. Mean M4 spans an 18-month period and comprises seven seasonal samples. Means were calculated by adding together raw data (as opposed to percentage data), then converting the raw data means to percentage relative abundances.

Code	M1	M2	M3	M4
Seasonal samples comprising 'mean' assemblage	July 1999 October 1999 January 2000 March 2000	October 1999 January 2000 March 2000 June 2000	January 2000 March 2000 June 2000 September 2000	May 1999 July 1999 October 1999 January 2000 March 2000 June 2000 September 2000

Table 6.9 Seasonal samples constituting 'mean' plankton assemblages M1 – M4

The DCA ordination diagram for all nine selected reservoirs (where seasonal diatom plankton samples were analysed) is illustrated in Figure 6.19. Figure 6.21 shows the same DCA ordination, but with the surface sediment sample(s) and mean annual diatom plankton assemblages (M1-M4) for each of the nine sites plotted passively and the individual seasonal samples hidden for clarity. Table 6.10 presents data on the DCA ordination space distances between the surface sediment sample(s) and each of the four mean annual diatom plankton assemblages (M1-M4) measured for the nine sites (measured from Figure 6.21 in standard deviation units). These distances provide an approximation for taphonomy (i.e. the disparity between live and fossil assemblages).

Overall, the mean phytoplankton assemblage for the period M1 (July 1999 – March 2000) is most similar to the fossil assemblage of the 0.5-1 cm surface sediment samples and thus a short distance separates these assemblages in DCA ordination space. In Upper Tamar, M1 (July 1999 - March 2000) is closest, perhaps in part reflecting the June 2000 date for the extraction of this site's 0.5-1 cm surface sediment sample. Upper Tamar's surface sediment sample can thus only comprise diatom remains laid down prior to June 2000. Period M4 represents the mean diatom plankton assemblage calculated for the entire 18 month period, July 1999 to September 2000. This period provides the second best approximation for the 0.5-1 cm fossil assemblage and provides the closest approximation for two reservoirs (Hollowell and Sutton Bingham – it is also joint closest for Chew Valley). The period M3, provides the third best approximation for the 0.5-1 cm fossil assemblage based on mean distances. However M3 has the shortest median distance and provides the closest approximation at two reservoirs (Porth and Tittesworth) and the joint closest at two other sites (Chew Valley and Blackbrook).

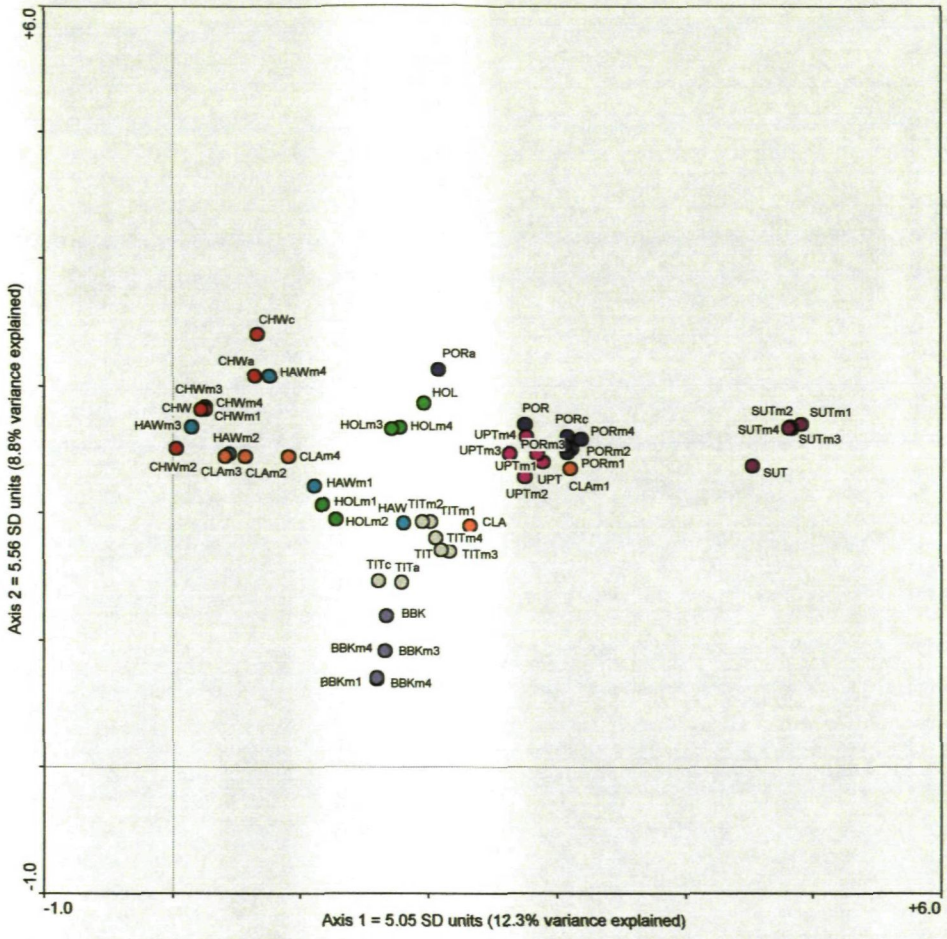


Figure 6.21 DCA ordination of seven seasonal diatom plankton assemblages in nine reservoirs, with passive mean seasonal assemblages M1-M4 (e.g. CHWm1-CHWm4) and surface sediment samples (e.g. CHW = 0.5-1 cm, CHWa = 0.5-1 cm, CHWc = 1-2 cm) illustrated. Modern samples and species are not shown, for these see Figure 6.19. See Appendix 2 for site codes)

Despite the observations noted above, the differences between the mean seasonal plankton assemblages (M1-M4) across all 9 reservoirs are not statistically significant. The degree of difference in ordination space between the four mean seasonal plankton assemblages and the 0.5-1 cm surface sediment sample assemblage from each of the 9 sites was statistically assessed using the Kruskal-Wallis non-parametric test. This gave a result of P = 0.689, indicating that the variation in distance between individual seasonal plankton means and the 0.5-1 cm surface sediment sample, is not greater than expected by chance. Therefore despite the mean diatom plankton assemblage M1 appearing in absolute value to provide the best approximation for the diatom assemblage recorded in the 0.5-1 cm sediment sample, this is not statistically significant.

Site	Surface sediment sample and mean seasonal diatom plankton sample Distance in ordination space (standard deviation units)											
	0 - 0.5cm				0.5 - 1cm				1 - 2cm			
	M1	M2	M3	M4	M1	M2	M3	M4	M1	M2	M3	M4
Blackbrook	-	-	-	-	0.50	0.27	0.27	0.50	-	-	-	-
Chew Valley	0.48	0.83	0.46	0.48	0.04	0.38	0.04	0.04	0.73	0.90	0.71	0.73
Clatworthy	-	-	-	-	0.88	1.83	2.00	1.50	-	-	-	-
Hawkridge	-	-	-	-	0.75	1.46	1.83	1.58	-	-	-	-
Hollowell	-	-	-	-	1.13	1.15	0.33	0.25	-	-	-	-
Porth	1.17	1.17	1.13	1.21	0.42	0.38	0.33	0.46	0.13	0.10	0.08	0.13
Sutton Bingham	-	-	-	-	0.50	0.44	0.44	0.42	-	-	-	
Tittesworth	0.54	0.50	0.46	0.46	0.25	0.27	0.06	0.10	0.63	0.58	0.63	0.54
Upper Tamar	-	-	-	-	0.08	0.17	0.25	0.23	-	-	-	-
Total distance	2.19	2.50	2.04	2.15	4.54	6.33	5.56	5.08	1.48	1.58	1.42	1.38
Mean distance	0.73	0.83	0.68	0.72	0.50	0.70	0.62	0.56	0.49	0.53	0.47	0.46
Median distance					0.50	0.38	0.33	0.42				
Standard deviation					0.36	0.61	0.75	0.58				
Closest			*		*							*

Table 6.10 **Distance in ordination space between the mean planktonic diatom assemblages (M1-M4) and the surface sediment diatom assemblages (0-0.5 cm, 0.5-1 cm and 1-2 cm) at 9 selected reservoirs.**

The period M3 (January 2000 – September 2000) appears to provide the best overall representation of the fossil assemblage of the 0-0.5 cm surface sediment sample. This is not perhaps surprising given that the top 0.5 cm of accumulated sediment is expected to represent the most recently sedimented phytoplankton remains. As seen in section 6.7, this sample is often a seasonal artefact, particularly in highly productive reservoirs with correspondingly high sedimentation rates. The period M4 (May 1999 – September 2000) appears to provide the best overall representation of the fossil assemblage seen in the 1-2 cm sediment sample, suggesting that this sample comprises diatom assemblages laid down over a longer time period. Caution has been taken to avoid over-interpretation of these observations, and no statistical tests have been performed because results are based on data from only three reservoirs. Analysis of further samples from a broader range of reservoirs (0-0.5 cm, 0.5-1 cm and 1-2 cm sediment samples in conjunction with seasonal plankton data) is recommended to enable more robust conclusions to be drawn.

6.7 Influence of diatom plankton seasonality on surface sediment diatom assemblages

To investigate the influence of diatom plankton seasonality and subsequent breakage and dissolution upon the representation of different diatom taxa lain down in the surface sediments, the diatom assemblage data from seasonal plankton samples were examined in conjunction with that from 0-0.5 cm, 0.5-1 cm and 1-2 cm depth sediment samples. This

was carried out for 3 selected reservoirs – Chew Valley, Porth and Tittesworth. Figures 6.22 illustrate the results of this analysis.

6.7.1 Chew

Figure 6.22a illustrates that during the period May 1999 – October 2000, *F. crotonensis* dominated Chew reservoir's diatom plankton assemblage. However in September 2000 the reservoir experienced a moderately-sized bloom of *A. granulata*. This bloom was captured in the 0-0.5 cm surface sediment sample taken at the same time, where the percentage relative abundance of *A. granulata* is much higher (34%) than in the 0.5-1 cm (13%) and 1-2 cm (8%) depth samples. In contrast, the percentage relative abundance of *F. crotonensis* is uncharacteristically low at 38%, while its representation in the plankton was consistently high at 60–90%. The 0.5-1 cm sediment sample provides a better representation of the period May 1999 – October 2000, since *F. crotonensis* is present at approximately 60% relative abundance, which is consistent with its mean relative abundance across the seven seasonal plankton samples. It is also consistent with the proportion of *F. crotonensis* present in the July 1999 plankton sample, the largest bloom in terms of cell concentrations recorded during the current study.

A. granulata var. *angustissima* is absent from all seasonal plankton assemblages, however it is present in all surface sediment samples. It occurs at highest relative abundance in the 1-2 cm sediment slice. This suggests that a large bloom of *A. granulata* var. *angustissima* occurred prior to the onset of seasonal plankton sampling in this study or produced a short-lived, large population between seasonal plankton samples. Evidence for the intensity of *A. granulata* var. *angustissima* blooms is provided by the single-species bloom of this taxon seen in May 1999 in the plankton of Hawkridge reservoir (Figure 7.7). *F. capucina* var. *mesolepta* is present at moderate relative abundance and cell concentrations in the May 1999 plankton sample, however it was found only at low relative abundance in the surface sediment samples (0-1%). Its low representation in the surface sediment samples is probably due to its low overall annual cell concentrations in the plankton compared to those of *F. crotonensis* and *A. granulata* var. *angustissima*. *C.* cf. *tholiformis* is either absent (0-0.5 cm sample) or at very low relative abundance (0.2% and 0.7% in the 0.5-1 cm and 1-2 cm samples respectively) in the surface sediment samples. However it is present at 7% in the largest absolute (in terms of cell concentration) plankton sample (July 1999). The reason for this may be that this species has a shorter growth period relative to the dominant planktonic taxa, thus only relatively small overall numbers of cells reach the sediments.

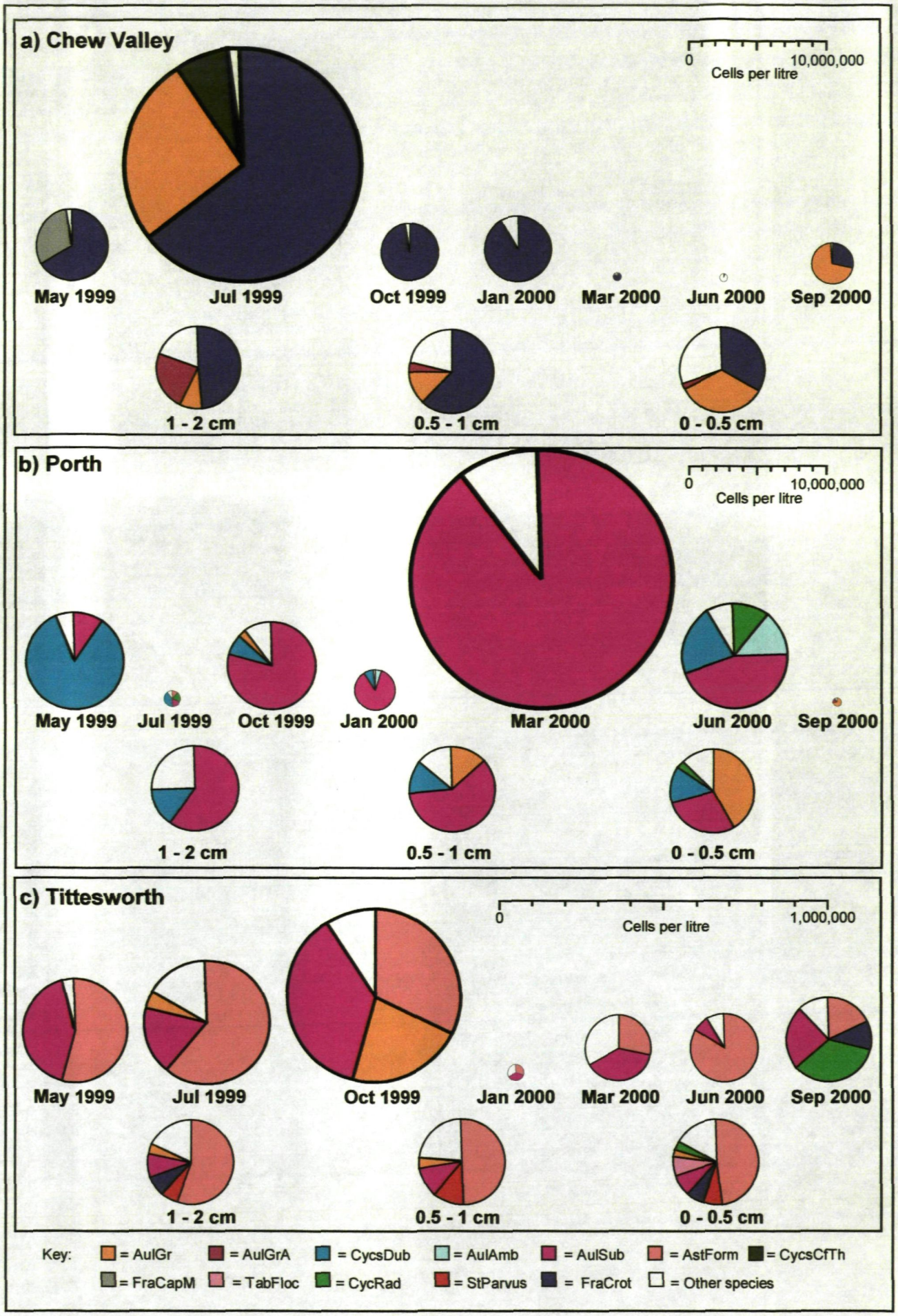


Figure 6.22 Percentage relative abundance of the dominant planktonic diatom taxa (>3%) in seasonal plankton samples and different depth surface sediment samples. Seasonal charts are drawn in proportion to cell concentrations (within each site).

6.7.2 Porth

A. subarctica is the dominant diatom taxon present in Porth reservoir's plankton over the period May 1999 – October 2000 (Figure 6.22b), occurring at a relative abundance of 10-90% (mean 50%). However, in common with Chew reservoir, a different taxon, in this case *A. granulata,* dominated the plankton in September 2000 (73% relative abundance). Once again this is reflected in the 0-0.5 cm sediment sample, where *A. granulata* occurs at the highest percentage relative abundance (43%), and *A. subarctica* occurs at only 30%, when in the 0.5-1 cm and 1-2 cm samples it is present at approximately 60% relative abundance. *A. granulata* appears to be overrepresented in the 0-0.5 cm sediment sample, particularly since the September 2000 bloom of *A. granulata* is small in terms of cell concentrations compared with that in March 2000 dominated by *A. subarctica*. However, *A. granulata's* presence in both the 0-0.5 cm and 0.5-1 cm samples suggests that a substantial bloom of this taxon between June 2000 and the end of October 2000 (when the September 2000 plankton sample was actually taken) was not captured by the coarse plankton sampling carried out in this study.

6.7.3 Tittesworth

Figure 6.22c illustrates that *A. formosa* and *A. subarctica* consistently dominate Tittesworth reservoir's planktonic diatom assemblage. *F. crotonensis* and *S. parvus* are consistently present in both the seasonal plankton samples and the surface sediment samples at relatively low percentages. However, they appear to have a greater relative abundance in the surface sediments than in the seasonal plankton samples, suggesting that seasonal blooms of these species were not captured by the coarse sampling frequency of the plankton in the current study. This is supported by the capture of a small bloom of *F. crotonensis* in the September 2000 plankton sample, but the absence of any significant blooms of *S. parvus* in any seasonal plankton sample. From the seasonal plankton data, *C. radiosa* is present at greatest relative abundance in September 2000. It is also present at its highest relative abundance in the 0-0.5 cm sediment sample. However, this is at only 3% relative abundance, compared with 33% in the September 2000 plankton sample. In addition, *C. radiosa* is present at 2% and 1% respectively in the 0.5-1 cm and 1-2 cm sediment samples, suggesting that the 0-0.5 cm sediment sample is representative of more than merely a seasonal artefact.

In Tittesworth, there does not appear to be the same seasonal artefact in the surface sediments evident in Chew and Porth. The reasons for this could be two-fold: a) the reservoir is less productive and exhibits a lower sedimentation rate than that seen in Chew and Porth. This is supported by the diatom concentration data, which indicate that the

concentration of Tittesworth's diatom plankton is between 10 and 100 times lower than that seen in Chew and Porth; b) The surface sediment sample taken from Tittesworth could have undergone either bioturbation or mechanical disturbance, leading to integration of sediment from different depths in the profile and hence a smoothing of the species compositional data. The former observation is more plausible since it is supported by the plankton concentration data.

6.8 Considerations relating to selection of appropriate surface sediment samples

Each individual reservoir's sedimentation rate will have a considerable influence upon the time periods represented by different 'surface' sediment slices. In those sites where diatom plankton productivity and hence sedimentation rates are low, the top 0-0.5 cm sediment sample may be most representative of the reservoir's annual diatom plankton populations (e.g. Tittesworth). However, in sites where phytoplankton productivity and sedimentation rates are high (e.g. Chew, Porth and Upper Tamar), the top 0-0.5 cm sediment sample may be insufficient to capture a reservoir's annual wax and wane of different planktonic diatom species. If this is the case, then the relationship between surface sediment diatom assemblages and *mean annual* epilimnetic chemistry may break down. It would perhaps be of benefit to pursue further combined analyses of surface sediment samples and seasonal diatom plankton from sites showing differing sedimentation rates. This information may lead to improvements in the selection of representative, annually integrated surface sediment samples for inclusion in calibration sets, perhaps reducing the likelihood of including surface sediment samples dominated by recent seasonal artefacts.

The above results could also be a product of the crude seasonal plankton sampling strategy adopted in this study. Only seven samples were taken at approximately two monthly intervals over the period May 1999 to October 2000, hence some diatom species blooms appear not to have been captured. Results indicate that in productive lowland reservoirs with high sedimentation rates, representative surface sediment samples are best taken from below 0.5 cm to reduce the influence of seasonal artefacts. On the basis of these findings, 0.5-1 cm depth surface sediment samples were selected for diatom analysis and subsequent inclusion in the UK lowland reservoirs calibration set. It is recognised that this is a compromise and that for different sites the 0.5-1 cm sample will represent slightly different time periods. However the decision is considered sound and justifiable based on the findings presented in this chapter.

In this study, surface sediment samples were primarily extracted in September / October 2000. As discussed above and by Sayer (2001), 0-0.5 cm surface sediment samples taken at this time often comprise diatom assemblages from the late summer / autumn bloom. A further investigation into the most appropriate time for surface sediment sampling could incorporate analyses of 0-0.5 cm surface sediment samples taken at different time of the year. However, the results of Tibby (2004) indicated that the day of the year on which surface sediment samples (0-0.5 cm slices) were taken, did not explain a significant amount of variation in surface sediment diatom assemblage composition. In addition, logistical constraints often feature prominently in the design of sampling strategies and calibration sets usually consist of a large number of sites that must be visited on at least one occasion, in part optimised for data quality but frequently constrained by logistics. With logistical considerations in mind, it is perhaps more appropriate to acknowledge the influence of seasonality on surface sediment assemblages and to account for this through analysis of the surface sediment sample considered most representative of the annual cycle in the system being studied e.g. perhaps 0.5-1 cm for productive lowland systems, but 0-0.5 cm for less productive reservoirs with lower sedimentation rates. Alternatively, provided the sample is well homogenised, a 0-1 cm sediment slice may provide the most representative sample across a range of systems where sedimentation rates are unknown and potentially variable.

The results discussed in section 6.6 suggested that the mean diatom plankton period M1 (July 1999 – March 2000) was the closest in terms of species composition to that laid down in the 0.5-1 cm sediment sample. This may indicate that period M1 is also the most suitable period over which to average the environmental data associated with the 0.5-1 cm surface sediment samples taken in September 2000 and used in the creation of inference models in the ensuing chapter. However the data from only nine sites have been used to draw this conclusion and the variation displayed between sites is high, with statistical tests showing that between-site variation is greater than that recorded between the means M1-M4.

Analysis of diatom plankton seasonality and reservoir sedimentation rates may improve selection of the most appropriate surface sediment sample and associated seasonal water chemistry data used to create diatom-based calibration sets. However data from the nine selected sites has indicated that the extra logistical expense and analytical endeavour to determine the most appropriate samples to use may not be warranted, particularly bearing in mind other errors inherent in the creation of inference models (see Chapter 9).

6.9 Summary points

- DCA indirect gradient ordination of the seasonal diatom plankton data for nine selected reservoirs suggests that many taxa demonstrate defined seasonal preferences. As a consequence, taxa are arranged in a cyclical pattern within the ordination space. Analysis of seasonal plankton samples from additional sites is required to further substantiate these observations.
- CCA direct gradient ordination of the seasonal diatom plankton and environmental data for nine selected reservoirs suggests that water clarity (SD), silica (Si), conductivity (EC) and pH are the most influential environmental variables in determining seasonality in planktonic diatom composition.
- Seasonal environmental data indicate that, at most sites, Si concentrations follow an inverse trend to Chla and Temp, decreasing most markedly following the spring diatom bloom and recovering in the autumn and winter.
- Some sites, such as Hollowell, Porth and Hawkridge support sequential, predominantly single-species diatom blooms. Other sites, such as Upper Tamar, Sutton Bingham and Tittesworth normally support diverse species assemblages, with blooms co-dominated by two or more taxa.
- The extent of inter-annual variation in seasonal planktonic diatom species assemblages differs greatly between sites.
- Some sites are dominated by diatoms e.g. Chew Valley and Sutton Bingham. At these sites seasonality in diatom populations is less pronounced. In other sites, e.g. Blackbrook and Hollowell, greater competition for resources between algal groups appears to influence the seasonality and definition of diatom populations.
- Weekly Water Company data available for some sites indicates that diatom blooms are often short-lived and are therefore sometimes missed or underestimated in this study's coarse phytoplankton sampling scheme.
- Diatom taxa typically seen to bloom during the spring include *A. islandica*, *S. parvus*, *A. granulata* var. *angustissima* and *D. vulgaris*. Taxa blooming in both the spring and late summer/autumn mixing periods include *A. formosa*, *A. subarctica* and *A. subarctica* fo. *subborealis*.
- Diatom taxa more typical of the summer and autumn period include *C. radiosa*, *C. meneghiniana*, *F. crotonensis*, *C. dubius*, *C.* cf. *tholiformis*, *C. invisitatus*, *A. normanii fo. subsalsa*, *A. granulata*, *S. neoastraea*, *S.* cf. *agassizensis*, *S. acus* and *T. flocculosa*.

- *F. crotonensis* blooms coincide with low SRP and Si concentrations. However it is uncertain from the current study whether this taxon is tolerant of such conditions, or whether its high cell concentrations strip the water column of both SRP and Si.
- Distances travelled in ordination space between seasonal planktonic diatom assemblages are shorter in the autumn/winter and longer in the summer. This can be explained because; a) winter planktonic diatom assemblages are frequently dominated by remnants of populations that bloomed in the autumn period and therefore the change in species composition between the autumn and winter plankton samples is only small; and b) over the summer period, larger shifts in diatom species composition occur, possibly owing to greater variations in ambient concentrations of key environmental variables at this time, leading to frequent changes in the competitive abilities of other algal species.
- In terms of diatom species composition, the mean diatom plankton period M1 (July 1999 – March 2000) provides the closest analogue to the diatom assemblage seen in the 0.5-1 cm sediment sample. However, statistical tests indicate that for the small sample of nine reservoirs, there was no significant difference between M1 and the other mean phytoplankton periods.
- The mean diatom plankton period M3 (January 2000 – September 2000) provides the best representation of the 0-0.5 cm sediment sample and the mean diatom plankton period M4 (May 1999 – September 2000) is closest in terms of its species composition to that seen in the 1-2 cm sediment sample. No tests of statistical significance of these results were performed due to the small sample size.
- In reservoirs where algal productivity and hence sedimentation rates are moderate to high (e.g. Chew Valley and Porth), the 0-0.5 cm sediment sample frequently comprises a 'seasonal artefact' i.e. a high relative abundance of taxa dominant in the plankton immediately prior to sampling. This is often inconsistent with the dominant species, in terms of cell concentrations, present in the plankton over the year prior to sediment sampling. In reservoirs where algal productivity and hence sedimentation rates are low (e.g. Tittesworth), the seasonal artefact is less apparent.
- In reservoirs with moderate to high sedimentation rates, the 0.5-1 cm sediment sample may provide the best representation both compositionally and proportionally of the mean diatom populations recorded in the plankton. In reservoirs with low to moderate sedimentation rates, the 0-0.5 cm surface sediment sample may be more appropriate, and in systems where sedimentation rates are unknown, well-homogenised 0-1 cm sediment samples may provide the best compromise.

- Seasonal diatom plankton data (and that of other algal groups) is valuable for interpreting sedimentary diatom records, since it can provide useful information on diatom ecology that can help to explain species shifts over time.

CHAPTER SEVEN

Development of inference models

7.1 Introduction

In the previous chapter, a number of environmental variables were highlighted as showing potential for the generation of diatom-based inference models. This chapter describes the development of these models using both the full and plankton-only datasets. Inference models were created using the methods of weighted averaging both with (WA_{tol}) and without (WA) tolerance downweighting, and executed using both classical and inverse deshrinking methods. Models based on two-component weighted averaging partial least squares (WAPLS (2)) were also tested. The random error in the models, i.e. the root mean squared error of prediction (RMSEP) was estimated in each case using leave-one-out jack-knifing internal cross-validation (ter Braak & Juggins, 1993). To assess systematic differences, mean bias and maximum bias (Birks, 1998) were estimated by jack-knifing. Statistical techniques are described more fully in Chapter 2. The performance and predictive ability of the different models created in this study are discussed both in relation to one another and with reference to those published in the literature, with the aim of determining whether robust inference models can be derived from the UK lowland reservoir calibration set. There are also further discussions relating to diatom species distributions and possible explanations are provided for trends seen across the datasets.

7.2 Justification for inference model construction

On the basis of the data screening exercises carried out in Chapter 5 (constrained and partially constrained CCAs, variance partitioning and forward-selected CCAs), it was concluded that the variation in total phosphorus (TP), chlorophyll-*a* (Chla), secchi depth (SD), alkalinity (Alk), potassium (K) (and conductivity (EC)) account for a significant fraction of the variance in the diatom data for both the full and plankton-only datasets. It would be feasible to develop models based on each of the above-mentioned variables, but since there are only two main gradients in the screened diatom datasets – axis 1 is a water chemistry gradient and axis 2 is a reservoir morphology and biological productivity gradient - models based on variables correlated to the same axis may not yield much additional information. However, it might be expected that all the above variables would provide some further independent information about species distributions since all could describe significant independent variation unexplained by covariables in partial CCAs.

7.2.1 Total Phosphorus (TP)

TP explains a significant and relatively high percentage of the variation in the diatom species data (5.5% and 5.3% in constrained CCA for the full and plankton-only datasets respectively – Tables 5.5 and 5.18) and shows a moderately high λ_1/λ_2 ratio (0.422 and 0.385 respectively for the full and plankton-only datasets – Tables 5.5 and 5.18). However TP is not independently so influential in determining diatom species distributions as either ionic and bicarbonate concentrations or water clarity and biological productivity, since it displays a discrete contribution of only 2.1% in both the full and plankton-only datasets - Figures 5.7 and 5.13, indicating that TP shares over half its explanatory power with inter-correlated variables.

The overall aim of this study is to determine the potential of UK lowland reservoirs for the development of diatom-nutrient inference models; therefore it would be inappropriate to rule out the creation of a diatom inferred-total phosphorus (DI-TP) inference model at this stage, when it is clear that TP does play a significant role in determining species distributions. TP is an environmental variable whose increased concentrations are well documented in the literature as an anthropogenic cause of eutrophication, and TP has the potential to be manipulated through management techniques for the benefit of reservoir ecology. There are also many DI-TP inference models in existence for different world regions and lake types (e.g. Anderson & Rippey, 1994; Reavie *et al.*, 1995; Wunsum & Schmidt, 1995; Bennion *et al.*, 1996; Lotter *et al.*, 1998; Dixit *et al.*, 1999; Bradshaw & Anderson, 2001; Kauppila *et al.*, 2002; Tibby, 2004). This will enable a UK lowland reservoir DI-TP inference model's performance to be effectively compared and contrasted with these existing models, whilst also extending the coverage of lake typologies represented by DI-TP inference models.

7.2.2 Alkalinity (Alk), Conductivity (EC) and Potassium (K)

Alk and EC displayed strong relationships with diatom species distributions along CCA axis 1 for both the full and plankton-only datasets. According to ter Braak & Šmilauer (1998b) reliable inference models can be developed for environmental variables that yield a relatively high ratio of eigenvalues corresponding to the first two axes (λ_1/λ_2) when entered as sole variables in constrained CCA analyses. Alk showed the highest λ_1/λ_2 ratio (0.533 and 0.531 for the full and plankton-only datasets respectively – Tables 5.5 and 5.18) and explained the highest percentage variance in the diatom species data (7.1%, and 7.5% respectively – Tables 5.5 and 5.18), indicating that Alk demonstrates a sufficiently strong relationship with diatom species distributions to support the generation of inference models.

EC was removed from CCA ordinations during dataset screening due to its high variance inflation factor indicating covariation with other variables in the environmental dataset. However, since EC explains a high percentage of the variation in the diatom data (7.0% and 7.1% respectively for the full and plankton-only datasets – Tables 5.5 and 5.18) and shows the second highest λ_1/λ_2 ratio (0.531 and 0.507 for the full and plankton-only datasets respectively – Tables 5.5 and 5.18), it is comparable with Alk in its suitability for the development of inference models. Ultimately however, only Alk or EC should be utilised because of the similarities in the diatom responses to these variables.

It is likely that EC provides a better reflection of the impact of anthropogenic pollution than Alk, because although Alk and EC are both intimately linked to catchment geology, EC is more highly correlated with individual ion species than Alk (Table 4.5) indicating that EC provides information above and beyond catchment characteristics. EC can be more readily influenced by anthropogenic pollution such as sewage effluent, road salt or agricultural fertiliser inwash, as reflected in the higher concentrations of cations and anions such as Na^+, K^+ and Cl^- in reservoirs affected by these forms of pollution. It is also preferable in this study to construct a model to infer EC since this proxy has the potential to provide useful information relating to changes in anthropogenic pollution over time, when applied to diatom sequences from individual sites. There are also a number of published DI-EC inference models with which to compare and contrast the results of this study (e.g. Gasse *et al*, 1995; Reed, 1998; Ryves *et al.*, 2002).

Although K explains a relatively high percentage of variation in the diatom data, it shares much of its explanatory power with other variables. K is just one of the cations contributing to the overall ionic concentration of the water and it is considered unwise to single out the effect of an individual ion species from the influence of overall ionic concentration and draw ecologically meaningful inferences. Therefore in this study it is not considered appropriate to develop a model solely for inferring K concentrations.

7.2.3 Chlorophyll-*a* (Chla) and Secchi Depth (SD)

Chla and SD were highly correlated with CCA axis 2, but in opposing directions for both the full and plankton-only datasets. Chla explained a high percentage of the variation in the diatom data (5.7% and 5.3% respectively for the full and plankton-only datasets – Tables 5.5 and 5.18) and shows a moderately high λ_1/λ_2 ratio (0.469 and 0.382 for the full and plankton-only datasets respectively – Tables 5.5 and 5.18). SD was comparable in its explanatory power, describing 5.4% and 6.0% (Tables 5.5 and 5.18) of the variation in the

diatom data respectively and showing high λ_1/λ_2 ratios of 0.468 and 0.457 (Tables 5.5 and 5.18) respectively for the full and plankton-only datasets. Both SD and Chla were significant in their independent influence over diatom species distributions (discrete contributions of >5% for both variables for both the full and plankton-only datasets - Figures 5.7 and 5.13).

The results for both DCAs and CCAs (Chapter 5) of the full and plankton-only datasets indicated that, although the first ordination axis explains the greatest proportion of variance, the second axis explains only slightly less. These results suggest that it would be appropriate to develop inference models for Chla and/or SD because each is a representative of the second axis of variation in the diatom data. However, since both variables represent the same axis of variation in the full and plankton-only datasets, it is concluded that it is probably inappropriate to construct models for both. Since SD can be affected by turbidity as well as biological productivity, Chla may generate a more ecologically relevant and meaningful model for inferring changes in biological phenomena.

It is recognised that the diatom taxa are partially generating the Chla gradient (in combination with other algal species) and are therefore a product of and not a response to Chla. As such, diatom taxa do not have Chla concentrations that are 'optimal' for growth (although Chla 'optima' will be referred to in ensuing discussions). In contrast to the data presented by Jones & Juggins (1995), the species' responses to Chla in the lowland reservoir calibration set are not directly related to the nutrient gradient and cannot therefore be interpreted as a nutrient proxy. This was shown in Chapter 4 by the weak relationships exhibited between TP and Chla (Figure 4.7a), and TN and Chla (Figure 4.7b). In addition, nutrients and Chla are related to different axes of variation in the diatom data: TN and TP are closely related to water chemistry variables, such as lake water ionic concentration and bicarbonate-carbonate status, whereas Chla is highly correlated with water clarity and lake morphometry and can therefore be seen as a proxy for these measures.

Although the diatom populations show a significant correlation with the Chla gradient, the usefulness of a Chla inference model is brought into question when it is clear that Chla is more intimately related to reservoir morphology than to a water quality parameter, such as the concentration of an individual nutrient. This is of potential relevance in terms of reservoir management and may raise issues concerning the ability to manipulate UK lowland reservoirs and their catchments to meet water quality targets. These issues will be discussed further in the following chapters.

7.3 Data transformations for the environmental and species data

7.3.1 Environmental variables

In Chapter 4, TP and Chla were shown to have non-normal positively skewed distributions (Figures 4.3a and 4.3c). The skew was successfully reduced using a $\log_{10}$ transformation (Table 4.6) and as such the environmental data used to create the TP and Chla inference models have been $\log_{10}$ transformed. Either $\log_{10}$ transformed data or the back-transformed values (or both) are presented.

EC demonstrated an approximately normal distribution across the full dataset (Table 4.6) and was therefore untransformed for indirect and direct gradient analyses (Chapter 5). However, as illustrated in section 7.6.1, when a preliminary inference model was created using non-transformed EC data, the graphical display of results indicated that $\log_{10}$ transformation of the data is advisable to reduce the skew and improve the inference model's performance statistics. EC data were thus $\log_{10}$ transformed for DI-EC model generation.

Table 7.1 illustrates the back-transformed descriptive statistics for the three environmental variables for which diatom-based inference models are constructed in the following sections of this chapter.

Variable (units)	Dataset	Hill's N^2	Min	Max	Mean	Median	St.Dev
EC (μScm^{-1})	Full	36.53	119.00	781.00	424.00	417.00	164.00
	Plankton	34.90	119.00	781.00	413.68	412.50	158.07
TP (μgl^{-1})	Full	40.57	12.00	242.00	62.50	67.48	2.18
	Plankton	38.66	12.00	242.00	62.50	67.48	2.16
Chla (μgl^{-1})	Full	37.39	1.80	25.50	5.76	5.65	1.85
	Plankton	35.84	1.80	25.50	5.94	5.80	1.83

Table 7.1 Back-transformed descriptive statistics for the environmental variables considered for inference model development (EC, TP and Chla).

7.3.2 Species

To reduce the influence of rare species in the performance statistics of inference models, only diatoms that occurred in at least two sites, with a relative percentage abundance of $\geq$1% in at least one site, were included (see Chapter 5). This resulted in an initial suite of 83 species in 42 sites for the full dataset and 39 species in 40 sites for the plankton-only dataset. When an outlier site was removed to improve inference model performance, the species dataset was re-examined and species failing to meet the above criteria were also removed.

ter Braak & Šmilauer (1998b) suggest that if species abundance values display a highly skewed distribution, a few high values can be prevented from unduly influencing the species ordinations by transforming the species data. Examination of the results of unconstrained ordinations (i.e. DCAs in Chapter 5) indicated that the surface sediment diatom assemblages of many calibration set sites are dominated by high relative percentage abundances of one or two taxa. To reduce the influence of these dominant taxa and to stabilise their variances, the diatom species data were square root transformed. The following section concerning the creation of DI-TP inference models, will discuss the use of square-root transformed (√) species data in more detail.

7.4 Development of DI-TP inference models for UK lowland reservoirs – comparative performance of different models.

7.4.1 Square-root transformed species data

The comparative results of preliminary TP inference models created for both the full (83 species, 42 site) and plankton-only (39 species, 40 site) datasets both before and after application of square-root transformations to the species data are displayed in Table 7.2.

Species	model	deshrinking method	r^2	r^2 jack	RMSE apparent (log_{10} µg l^{-1})	RMSEP jack (log_{10} µgl^{-1})	mean bias (jack) (log_{10} µgl^{-1})	maximum bias (jack) (log_{10} µgl^{-1})
All	WA	classical	0.60	0.33	0.28	0.34	0.017	0.340
	WA	inverse	0.60	0.30	0.21	0.29	0.010	0.315
	WA_{tol}	classical	0.57	0.33	0.30	0.29	0.056	0.357
	WA_{tol}	inverse	0.57	0.29	0.22	0.29	0.029	0.350
	WAPLS (2)	-	0.72	0.28	0.18	0.30	-0.004	0.326
All	WA	classical	0.69	0.46	0.23	0.28	-0.003	0.218
√species	WA	inverse	0.69	0.44	0.19	0.25	-0.004	0.255
	WA_{tol}	classical	0.53	0.46	0.32	0.26	0.069	0.309
	WA_{tol}	inverse	0.53	0.41	0.23	0.28	0.032	0.382
	WAPLS (2)	-	0.86	0.38	0.13	0.27	-0.016	0.239
Plankton	WA	classical	0.53	0.29	0.32	0.37	0.028	0.343
	WA	inverse	0.53	0.25	0.23	0.30	0.014	0.337
	WA_{tol}	classical	0.60	0.31	0.27	0.34	0.026	0.310
	WA_{tol}	inverse	0.60	0.26	0.21	0.29	0.015	0.356
	WAPLS (2)	-	0.60	0.22	0.21	0.31	0.001	0.355
Plankton	WA	classical	0.62	0.43	0.26	0.31	0.012	0.247
√species	WA	inverse	0.62	0.39	0.21	0.26	0.005	0.325
	WA_{tol}	classical	0.64	0.36	0.25	0.31	0.035	0.344
	WA_{tol}	inverse	0.64	0.33	0.20	0.28	0.020	0.389
	WAPLS (2)	-	0.75	0.29	0.17	0.30	-0.007	0.368

Table 7.2 Comparison of the performance statistics for DI-TP inference models created using non-transformed and square-root transformed (√) diatom species data for both the 42 site (full) and the 40 site (plankton-only) datasets. The best performing models are shaded.

The use of square-root transformed species data (√) resulted in improved model performance statistics for both the full and plankton-only datasets, and the extent of the

improvement in each individual model's performance were similar for both datasets. Of particular note were the reductions in prediction error for each model. Overall, the mean reduction in RMSEP for the full and plankton-only dataset models were 12% and 10% respectively. Comparably high levels of improvement for both datasets probably reflect the dominance of planktonic species, many of which display high variances and large tolerances, which resulted in poorly defined optima. The square root transformation (√) reduces the influence of these species, in turn enhancing overall inference model performance. As such, all subsequent models are constructed using square-root transformed (√) species data.

7.4.2 Linear (PLS) vs. unimodal (WA / WAPLS) models

Linear models based on partial least squares (PLS) were also developed. Performance statistics (not presented) indicate that the unimodal (WA / WAPLS) models outperform those based on linear techniques for the full dataset, and produce very similar results for the plankton-only dataset. Since the best performing PLS models give no appreciable improvement over the best WA and WAPLS models, PLS models are not considered further in this chapter.

7.4.3 Preliminary results using all species and sites in the full and plankton-only datasets (square-root transformed species data).

The performance statistics for the models created using the first WAPLS component (WAPLS (1)) were virtually identical to those created using WA inverse deshrinking because the first WAPLS component (WAPLS (1)) is equivalent to simple WA with inverse deshrinking (Bennion *et al.*, 1996). WAPLS (1) statistics are therefore not presented.

Table 7.2 and Figures 7.1a-e indicate that the best performing TP inference models for both the full and plankton-only datasets (using square-root transformed data) were those employing WA inverse deshrinking. The full dataset showed jack-knifed error statistics of $r^2_{jack} = 0.44$, RMSEP = 0.25 $\log_{10}$ μgl^{-1}, mean bias = -0.004 $\log_{10}$ μgl^{-1} and maximum bias = 0.255 $\log_{10}$ μgl^{-1}). The plankton-only dataset's performance was only slightly lower than that employing the full dataset, displaying very similar statistics of $r^2_{jack} = 0.39$, RMSEP = 0.26 $\log_{10}$ μgl^{-1}, mean bias = -0.005 $\log_{10}$ μgl^{-1} and maximum bias = 0.325 $\log_{10}$ μgl^{-1}).

Although the WA inverse deshrinking model produced the best performance statistics, inverse deshrinking methods underestimate TP at higher concentrations (Figure 7.1b); an

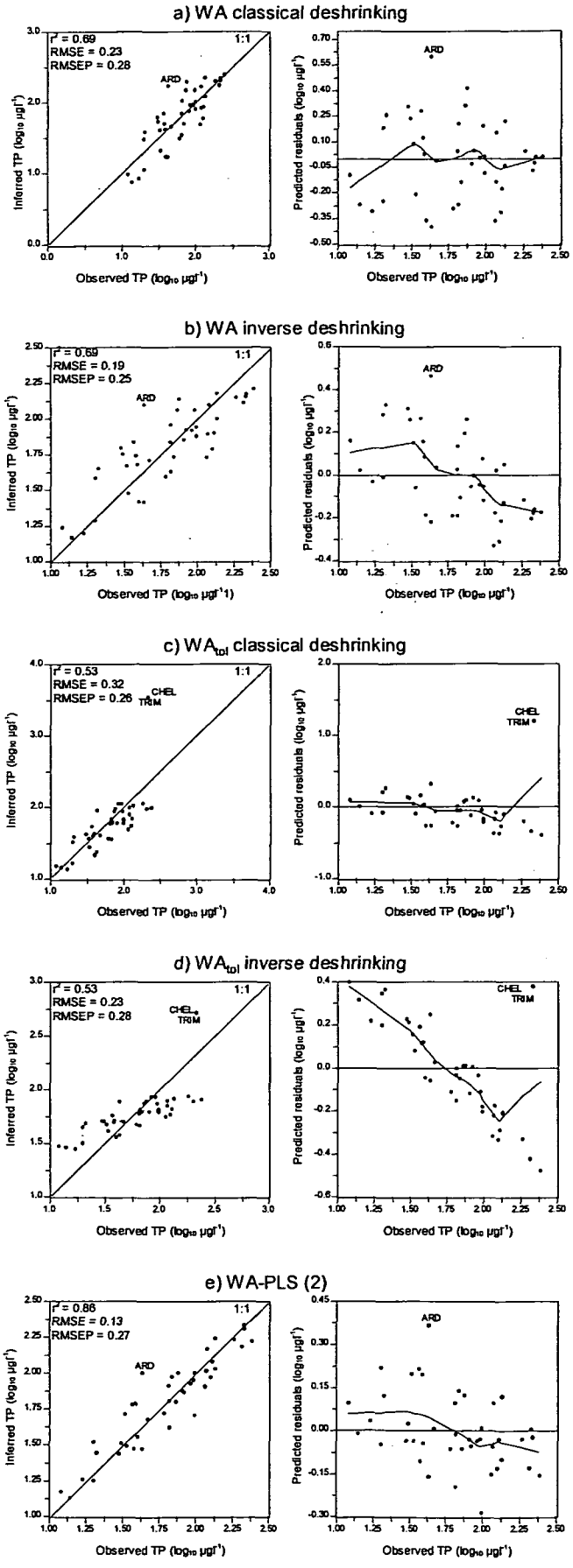
observation frequently reported by other authors (e.g. Hall & Smol, 1992; Anderson *et al.*, 1993 and Bennion *et al.*, 1996). This is due to the inherent bias in the model (Martens & Naes, 1989) and is not a reflection of biological factors, since the model created under WA classical deshrinking does not yield a similar trend (Figure 7.1a). The reduced trend in the residuals displayed by the models employing classical deshrinking indicate that these models are good at accurately inferring values towards the ends of the TP gradient. Application of these models might be appropriate at sites where inferred TP is expected to lie at either extreme of the TP gradient, or where inference of high or low TP concentrations is considered critical.

7.4.4 Identification of site outliers

Chelmarsh and Trimpley

Figures 7.1 a-e graphically represent the data displayed in Table 7.2. For the full dataset, Chelmarsh and Trimpley are clear outliers under the WA_{tol} classical model and fail to follow the general dataset trend under the WA_{tol} inverse model. The residuals of these sites are greater than the standard deviation for the dataset (0.34 $\log_{10}$ μgl^{-1} TP); Chelmarsh and Trimpley both display residuals of approximately 1.21 and 0.38 $\log_{10}$ μgl^{-1} TP under the WA_{tol} classical and inverse models respectively. The influence of these sites on the model performance statistics was assessed by removing both sites and re-running the WA and WAPLS models. In addition to removing these sites, it was necessary to remove two species from the models. One species (*Cymbella sinuata*) only occurred at these sites, and another species (*Surirella brebissonii*) failed to fulfil the species abundance criteria when both Chelmarsh and Trimpley were removed.

Following the removal of these sites and associated species, r^2_{jack} improved significantly for both the WA_{tol} classical and inverse models, indicating the improved fit of sites to the line of best fit. However the RMSEP values remained largely unimproved. Since the WA_{tol} models were shown to perform less well than the simple WA models, and since Chelmarsh and Trimpley were not shown to be outliers in these better performing models, it was decided *not* to remove these two sites from the dataset and risk the loss of possibly valuable ecological information. In addition, for the plankton-only dataset Chelmarsh and Trimpley were not considered to be outliers, further indicating that their outlier status was most probably determined by the presence of the non-planktonic taxon *C. sinuata* that occurred exclusively in these sites, and thus showed the highest TP optima of all species represented



Figures 7.1 a-e **Plots of observed vs. inferred and observed vs. residual mean TP concentrations (log_{10} μgl^{-1}) for the full dataset (species square-root transformed).**

in the dataset. Chelmarsh and Trimpley were therefore retained for inclusion in the final models generated for both the full and plankton-only datasets.

Ardleigh

For the full dataset Ardleigh appeared to be an outlier in the WA inverse deshrinking and WAPLS (2) models, both in terms of observed vs. inferred TP and predicted residuals (Figures 7.1 b and 7.1 e). Ardleigh did not visually appear to be such an extreme outlier as Chelmarsh and Trimpley in the WA_{tol} models. However its residuals for the WA classical and inverse deshrinking models (0.6 and 0.47 $\log_{10}$ μgl^{-1} TP respectively) were greater than the standard deviation of TP in the calibration set (0.34 $\log_{10}$ μgl^{-1} TP) (Jones & Juggins, 1995). A possible explanation for the overestimation of Ardleigh's TP concentration could stem from the phosphorus stripping, which is applied to the water entering the reservoir. The diatom assemblage seen in the reservoir's surface sediments (including *Actinocyclus normanii* fo. *subsalsa*, *Stephanodiscus neoastraea* and *Aulacoseira granulata*) is characteristic of sites with both high EC and TP concentrations. Phosphate stripping artificially lowers TP in Ardleigh to an annual average concentration of approximately 40 μgl^{-1} TP, but has no impact on the reservoirs conductivity. Consequently at Ardleigh there is a breakdown in the overall strong inter-correlation between EC and TP seen across the reservoirs dataset and thus an anomaly in the resultant species assemblage.

species	Model	deshrinking method	r^2	r^2 jack	RMSE apparent ($\log_{10}$ $\mu g\ l^{-1}$)	RMSEP jack ($\log_{10}$ μgl^{-1})	mean bias (jack) ($\log_{10}$ μgl^{-1})	maximum bias (jack) ($\log_{10}$ μgl^{-1})
All	WA	classical	0.73	0.54	0.21	0.25	-0.009	0.233
	WA	inverse	0.73	0.53	0.18	0.23	-0.007	0.241
	WA_{tol}	classical	0.59	0.58	0.29	0.23	0.060	0.320
	WA_{tol}	inverse	0.59	0.57	0.22	0.26	0.032	0.378
	WAPLS (2)		0.87	0.56	0.13	0.23	-0.003	0.099
Plankton	WA	classical	0.68	0.53	0.23	0.27	0.004	0.259
	WA	inverse	0.68	0.51	0.19	0.24	0.002	0.276
	WA_{tol}	classical	0.71	0.54	0.22	0.25	0.027	0.273
	WA_{tol}	inverse	0.71	0.52	0.18	0.23	0.018	0.355
	WAPLS (2)		0.80	0.53	0.15	0.24	0.020	0.238

Table 7.3 Performance of the different DI-TP models created using the full dataset (82 species, 41 sites) and the plankton-only dataset (38 species and 39 sites) - Ardleigh and *T. bramaputrae* removed from both datasets. The best performing models are shaded.

The removal of Ardleigh, along with the diatom taxon *Thalassiosira bramaputrae,* which failed to meet the abundance criteria following Ardleigh's removal, led to improvements in the full range of performance statistics for all models and not only improvements in the r^2 values as was evident following removal of Chelmarsh and Trimpley from the WA_{tol} models. For the full dataset, WA inverse deshrinking remained a strong performer, but

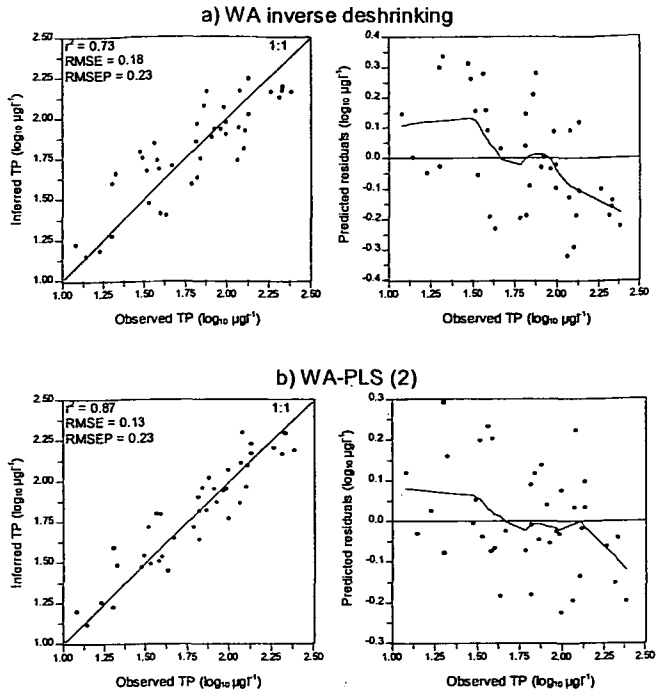


Figure 7.2a-b Plots illustrating observed vs. inferred and observed vs. residual annual mean TP (log_{10} μgl^{-1}) for the full dataset (82 species and 41 sites – minus Ardleigh and *T. bramaputrae*). Only plots for the best performing models (WA inverse deshrinking and WAPLS (2)) are shown.

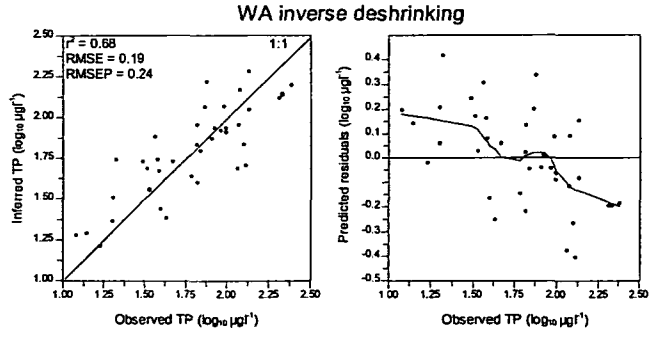


Figure 7.3 Plots illustrating observed vs. inferred and observed vs. residual annual mean TP (log_{10} μgl^{-1}) for the plankton-only dataset (38 species and 39 sites – minus Ardleigh and *T. bramaputrae*). Only plots for the best performing model (WA inverse deshrinking) are shown.

WAPLS (2) displayed a lower mean and maximum bias and a slightly lower RMSEP than the WA inverse deshrinking model (Table 7.3). Although the WAPLS (2) model gave the lowest RMSEP, the improvement was only 1-2% of the RMSEP for the simplest one-component model (WAPLS (1)), not attaining the level of improvement of 5% or more deemed necessary for a component to be considered 'useful' (ter Braak & Juggins, 1993; Birks, 1998; Brooks & Birks, 1999). However, since WAPLS (2) reduced mean bias, maximum bias and the trend in the residuals, the model was seen to be the best for inferring TP across the entire gradient covered by the full dataset. For the plankton-only dataset, Ardleigh was also highlighted as an outlier and removed in combination with *T.*

bramaputrae as for the full dataset. The best model in terms of a low RMSEP and low mean and maximum bias statistics was that using WA inverse deshrinking (Table 7.3). Improvements in model performance statistics following the removal of Ardleigh supported its exclusion from the development of a DI-TP model for both the full and plankton-only datasets.

7.4.5 Distributions, optima and tolerances of diatom species in the full and plankton-only datasets

Table 7.4 details the TP optima and tolerances of the diatom species included in both the full and plankton-only datasets. Figure 7.4 displays this data graphically for only the full dataset because the optima and tolerances of the planktonic species are overall similar whether calculated from the full or plankton-only dataset. There are only five planktonic taxa whose TP optima vary between datasets by >5 μgl^{-1}. Of these species, only three show a discrepancy of $\geq$10 μgl^{-1} (*Stephanodiscus hantzschii* fo. *tenuis*, -19; *Diatoma tenuis* var. *elongatum*, -10; *Diatom vulgaris*, +11). If the models were used for reconstruction purposes in reservoirs with a high abundance of one or more of these species, it might be expected that the plankton-only model would produce correspondingly divergent reconstructed TP values.

Species with the highest TP optima (>100 μgl^{-1}) include the planktonic taxa *A. normanii* fo. *subsalsa*, *Cyclotella meneghiniana*, *S. hantzschii* fo. *tenuis*, *Cyclotella atomus* and *Aulacoseira islandica*, and the periphytic taxa *C. sinuata*, *Gomphonema pumilum*, *Nitzschia amphibia*, *Gomphonema minutum*, *Gomphonema olivaceum* var. *minutissimum*, *Navicula lanceolata* and *Cocconeis pediculus*. Species with the lowest TP optima (<50 μgl^{-1}) include the planktonic taxa *Nitzschia gracilis*, *Synedra rumpens* var. *familiaris*, *Tabellaria flocculosa*, *Cyclotella ocellata*, *Synedra acus* var. *radians*, *Aulacoseira subarctica*, *Synedra acus* var. *angustissima*, *Asterionella formosa*, *Cyclotella radiosa*, *Aulacoseira ambigua* and *Fragilaria crotonensis*, and the non-planktonic taxa *Denticula kuetzingii*, *Nitzschia sinuata* var. *tabellaria*, *Fragilaria pinnata*, *Gomphonema olivaceum*, *Cymbella microcephala*, *Encyonema caespitosum* and *Achnanthes minutissima*.

Taxa with high TP optima and narrow tolerances include *C. sinuata*, *G. pumilum*, *A. normanii* fo. *subsalsa*, *A. islandica*, *Navicula capitata*, *G. olivaceum* var. *minutissimum*, *G. minutum* and *Aulacoseira granulata* var. *angustissima* fo. *curvata*, and those with a low TP optima and narrow tolerance include *G. olivaceum*, *S. acus* var. *angustissima* and *E. caespitosum*. Species with a high TP optima and broad tolerance include *Melosira varians*,

Surirella Brebissonii and *N. lanceolata*, and those with a low TP optima and broad tolerance include *D. kuetzingii*, *Gomphonema angustatum* and *F. pinnata*. Species with both the broadest and narrowest tolerances generally occur in only a small number of sites.

Figures 7.5a and 7.5b illustrate square-root transformed diatom species percentage relative abundance data ($\sqrt{\%}$) against annual mean TP concentration ($\log_{10}$ μgl^{-1} TP) for a) the full dataset (42 sites and 83 species) and b) the plankton-only dataset (40 sites and 39 species). Table 7.5 summarises the proportion of species exhibiting different response models, distributions having been determined by eye.

WA methods assume that species respond to a given environmental variable in a unimodal fashion, which is more consistent with ecological observations than linear models (ter Braak & van Dam, 1989). 35% (full dataset) – 41% (plankton-only dataset) of the species distributions can be classified as unimodal (symmetrical or asymmetrical). Species illustrating this distribution pattern include the planktonic taxa *A. granulata*, *Aulacoseira granulata* var. *angustissima*, *Aulacoseira subarctica* fo. *subborealis*, *A. islandica*, *Cyclostephanos* cf. *tholiformis*, *Cyclostephanos invisitatus*, *C. radiosa*, *A. normanii* fo. *subsalsa*, *S. neoastraea*, *S. hantzschii* fo. *tenuis*, *S. acus* var. *angustissima* and *S. acus* var. *radians*, and the periphytic taxa *G. olivaceum*, *Rhoicosphenia abbreviata*, *Nitzschia dissipata* and *N. capitata*. A higher percentage of planktonic taxa than periphytic taxa exhibit unimodal distributions, with less showing no clear trend to TP. Since WA methods assume unimodal response models, this may help to explain why the plankton-only model performs almost as well as that using both planktonic and periphytic taxa.

More species distributions were truncated at the upper end (25%) than the lower end (13%) of the TP gradient. Truncation at the upper end (sigmoidal increasing curve) indicates that the optima for these species are probably underestimated. Species displaying this trend include the planktonic species *Fragilaria capucina* var. *mesolepta*, *C. meneghiniana*, *C. atomus*, *Stephanodiscus* cf. *agassizensis*, *T. bramaputrae*, *D. vulgaris*, *M. varians*, *Nitzschia palea* and *Nitzschia fonticola*, and the periphytic species *S. brebissonii*, *Navicula cryptocephala*, *Achnanthes lanceolata*, *Nitzschia recta*, *N. lanceolata*, *C. pediculus*. These taxa are all typical of high TP sites, and further sampling of higher TP sites to extend the TP gradient of the calibration set might enable better estimation of their optima.

Taxon code	N	N	Max %	Max %	Hill's N2	Hill's N2	TP optima A	TP optima B	TP optima A	TP optima B	Tolerance A	Tolerance C	Tolerance D	Tolerance A	Tolerance C	Tolerance D
AchLan	24		1.48		20.40		1.961	92			0.356	52	115			
AchMin	36		2.45		28.40		1.681	48			0.342	26	57			
ActNormS	9	9	5.35	5.35	5.10	5.10	2.115	130	2.115	130	0.134	34	47	0.134	34	47
AmphInar	11		1.23		9.28		1.923	84			0.328	45	94			
AmphLib	26		1.30		22.32		1.868	74			0.338	40	87			
AmphPed	24		2.00		19.73		1.979	95			0.293	46	92			
AstForm	37	35	7.71	7.71	24.25	22.92	1.684	48	1.690	49	0.351	26	60	0.355	27	62
AulAmb	20	19	6.65	6.65	12.55	12.35	1.689	49	1.691	49	0.372	28	66	0.373	28	67
AulGr	21	21	6.50	6.50	13.37	13.37	1.917	83	1.917	83	0.246	36	63	0.246	36	63
AulGrA	18	16	5.21	5.21	12.20	11.48	1.850	71	1.848	70	0.244	31	53	0.236	29	51
AulGrACu	2	2	1.65	1.65	2.00	2.00	1.944	88	1.944	88	0.028	6	6	0.028	6	6
AulIslan	4	4	5.57	5.57	3.33	3.33	2.009	102	2.009	102	0.167	32	48	0.167	32	48
AulSub	19	18	7.71	7.71	14.46	14.28	1.640	44	1.641	44	0.347	24	53	0.348	24	53
AulSubB	5	5	6.55	6.55	2.77	2.77	1.920	83	1.920	83	0.181	28	43	0.181	28	43
CocPed	16		1.64		13.41		2.003	101			0.304	51	102			
CocPlac	36		3.30		23.61		1.902	80			0.356	45	101			
CycAtm	12	12	3.28	3.28	8.78	8.78	2.014	103	2.014	103	0.269	47	89	0.269	47	89
CycMeng	19	17	2.79	2.79	13.08	11.59	2.061	115	2.060	115	0.276	54	102	0.269	53	98
CycOcel	3	3	1.64	1.64	2.41	2.41	1.626	42	1.626	42	0.274	20	37	0.274	20	37
CycPseu	27	26	4.25	4.25	19.42	18.53	1.945	88	1.933	86	0.303	44	89	0.302	43	86
CycRad	29	28	4.61	4.61	21.75	21.37	1.682	48	1.676	47	0.304	24	49	0.299	23	47
CycsCfTh	15	13	2.81	2.81	10.85	9.64	1.883	76	1.877	75	0.258	34	62	0.243	32	57
CycsDub	23	21	6.33	6.33	16.46	15.83	1.916	82	1.920	83	0.279	39	75	0.276	39	74
CycsInv	28	26	4.97	4.97	17.75	16.16	1.973	94	1.964	92	0.261	42	77	0.244	40	69
CymMic	8		1.08		7.35		1.617	41			0.374	24	57			
CymSin	2		1.23		1.83		2.334	216			0.001	0	0			
DenKuet	3		1.58		2.01		1.432	27			0.651	21	94			
DiatTenE	10	9	1.31	1.31	8.16	7.20	1.714	52	1.620	42	0.401	31	78	0.347	23	51
DiatVul	13	12	1.68	1.68	10.77	9.78	1.932	85	1.982	96	0.355	47	109	0.337	52	112
DipPar	17		1.97		13.43		1.706	51			0.406	31	78			
EncyCaes	4		1.03		3.84		1.666	46			0.201	17	28			
EncySil	29		1.60		23.71		1.768	59			0.338	32	69			
FraBrev	14		3.44		10.57		1.871	74			0.358	41	95			
FraCapM	16	15	1.73	1.73	13.33	12.33	1.881	76	1.914	82	0.325	40	85	0.315	42	87
FraConB	6		1.53		4.48		1.843	70			0.347	39	85			
FraCrot	26	26	8.51	8.51	17.35	17.35	1.698	50	1.698	50	0.346	28	61	0.346	28	61
FraEllip	9		2.32		7.68		1.856	72			0.375	42	98			
FraPinn	5		1.92		3.79		1.560	36			0.440	23	64			
FraVau	31		2.49		25.27		1.835	68			0.352	38	86			
GomAng	2		1.13		1.73		1.753	57			0.641	44	191			
GomMint	10		1.48		8.28		2.078	120			0.214	47	76			
GomOli	7		1.46		5.67		1.574	38			0.205	15	22			
GomOliM	6		1.52		4.77		2.037	109			0.193	39	61			
GomPar	25		1.08		22.80		1.770	59			0.360	33	76			
GomPum	2		1.23		1.65		2.193	156			0.190	55	86			
GyroAcc	32		1.68		27.58		1.779	60			0.343	33	72			
MelVar	21	19	1.85	1.85	16.91	15.21	1.963	92	1.978	95	0.366	52	121	0.360	54	123
NavCap	8		1.09		7.06		1.954	90			0.175	30	45			
NavCapr	24		1.25		21.16		1.825	67			0.344	37	81			
NavCari	9		1.12		8.06		1.925	84			0.360	47	109			
NavCrypt	17		1.47		14.66		1.933	86			0.390	51	124			
NavExil	4		1.67		3.62		1.762	58			0.395	35	86			
NavGreg	28		2.30		23.36		1.837	69			0.363	39	89			
NavLanc	22		2.58		15.89		2.003	101			0.346	56	122			
NavMen	30		1.12		27.80		1.849	71			0.319	37	76			
NavPslan	6		2.22		4.67		1.820	66			0.316	34	71			
NavPup	13		0.98		12.23		1.861	73			0.329	39	82			
NavTrip	12		1.40		10.43		1.991	98			0.326	52	109			
NavVen	16		1.41		13.22		1.711	51			0.363	29	68			
NitzAmp	10		1.07		8.89		2.117	131			0.181	45	68			
NitzDis	25		1.27		21.79		1.877	75			0.301	37	76			
NitzFont	19	17	2.90	2.90	13.50	12.00	1.951	89	1.960	91	0.358	50	115	0.354	51	115
NitzGrac	7	7	1.14	1.14	6.80	6.80	1.425	27	1.425	27	0.293	13	25	0.293	13	25
NitzPal	19	18	1.37	1.37	16.50	15.51	1.965	92	1.947	89	0.318	48	100	0.318	46	95
NitzRec	26		1.04		23.27		1.941	87			0.314	45	93			
NitzSinT	3		1.87		2.46		1.494	31			0.304	16	32			
RhAbbrev	28		3.03		20.09		1.958	91			0.300	46	90			
StAlp	6	6	2.79	2.79	4.86	4.86	1.844	70	1.844	70	0.329	37	79	0.329	37	79
StCfAgas	24	24	4.89	4.89	18.12	18.12	1.974	94	1.974	94	0.294	46	91	0.294	46	91
StHantz	22	21	3.28	3.28	15.85	14.94	1.849	71	1.812	65	0.343	39	85	0.333	35	75

Taxon code	N	n	Max %	Max %	Hill's N2	Hill's N2	TP optima A	TP optima B	TP optima A	TP optima B	Tolerance A	Tolerance C	Tolerance D	Tolerance A	Tolerance C	Tolerance D
StHantzT	15	14	4.93	2.70	8.49	10.87	2.012	103	1.923	84	0.267	47	87	0.245	36	63
StNeo	21	21	3.84	3.84	15.89	15.89	1.969	93	1.969	93	0.266	43	79	0.266	43	79
StParvus	37	36	5.25	5.25	27.99	27.37	1.792	62	1.797	63	0.325	33	69	0.326	33	70
SurBreb	11		0.97		10.00		1.966	93			0.362	53	120			
SurMin	12		1.00		10.70		1.766	58			0.346	32	71			
SynAcA	4	4	1.17	1.17	3.53	3.53	1.652	45	1.652	45	0.144	13	18	0.144	13	18
SynAcR	11	11	1.31	1.31	9.31	9.31	1.632	43	1.632	43	0.280	21	39	0.280	21	39
SynRuFa	2	2	1.82	1.82	1.94	1.94	1.448	28	1.448	28	0.263	13	23	0.263	13	23
SynRuFr	4	3	1.39	1.39	3.29	2.46	1.825	67	1.724	53	0.362	38	87	0.312	27	56
SynRump	11	10	1.24	1.24	9.55	8.80	1.812	65	1.787	61	0.431	41	110	0.430	38	104
SynRuSc	2	2	1.74	1.74	1.66	1.66	1.881	76	1.881	76	0.175	25	38	0.175	25	38
TabFloc	6	6	3.29	3.29	3.72	3.72	1.511	32	1.511	32	0.372	18	44	0.372	18	44

Table 7.4 **TP WA diatom species optima and tolerances calculated from the full (82 species, 41 sites) and plankton-only (38 species, 39 sites) datasets with Ardleigh and *T. bramaputrae* removed. Shaded columns indicate data for the plankton-only dataset. A = log_{10} transformed TP (log_{10} μgl^{-1}); B, C and D = back-transformed TP (μgl^{-1}); C = lower tolerance when back-transformed, D = higher tolerance when back-transformed.**

Species distribution	Full dataset number	%	Plankton-only dataset number	%
Unimodal	29	**35**	16	**41**
Truncated (lower end)	11	**13**	7	**18**
Truncated (upper end)	21	**25**	10	**26**
No clear trend	22	**27**	6	**15**

Table 7.5 **Classification of diatom species distributions in relation to TP for both the full and plankton-only datasets.**

TP optima for species distributions truncated at the lower end of the TP gradient (sigmoidal decreasing curve) probably have overestimated optima. These species include *N. gracilis*, *T. flocculosa*, *C. microcephala*, *A. minutissima*, *D. kuetzingii* and *F. pinnata*. Taxa such as *A. formosa*, *A. subarctica*, *A. ambigua* and *F. crotonensis* have distributions that may be truncated. However it is unclear whether their optima are truly overestimated, or whether they simply have a broad tolerance for TP. Since they occur in sites spanning the TP gradient, this may indicate that their distributions are largely determined by environmental variables other than TP and could perhaps be classified as showing no clear response to TP. These are some of the most commonly occurring taxa in the dataset and all have moderate to high effective abundances (Hill's N^2 = 12-23 (Table 7.4)). If they do show little response to TP, this may be significant in assessing the robustness of their derived optima, perhaps raising issues concerning the predictive ability and hence usefulness of the DI-TP models in sites where diatom records are dominated by species broadly tolerant to TP. These issues will be raised further when the models are applied to core sequences in Chapter 8.

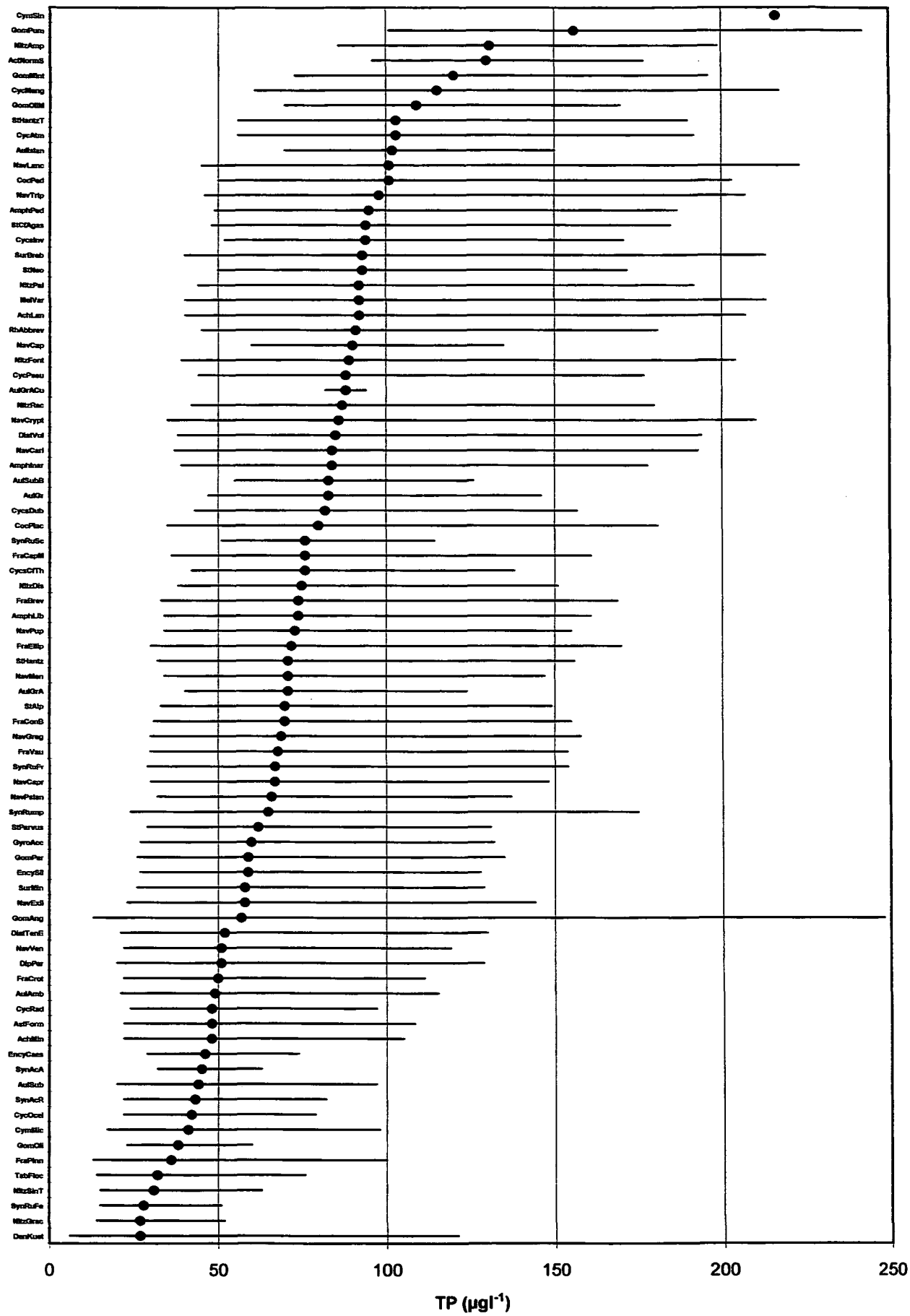


Figure 7.4 **TP optima and tolerances for the full dataset of 83 species and 42 sites. Species are ordered according to WA TP optima.**

Figures 7.5a Plots illustrating square-root transformed diatom species percentage relative abundance (√ %) against annual mean TP concentration (log_{10} μgl^{-1} TP) for the full dataset (42 sites and 83 species) Tick marks show the estimated WA TP optima for each species and the curves show the modelled response under logistic regression (LOGIT) (predicted unimodal fit). Species are ordered from low to high TP optima.

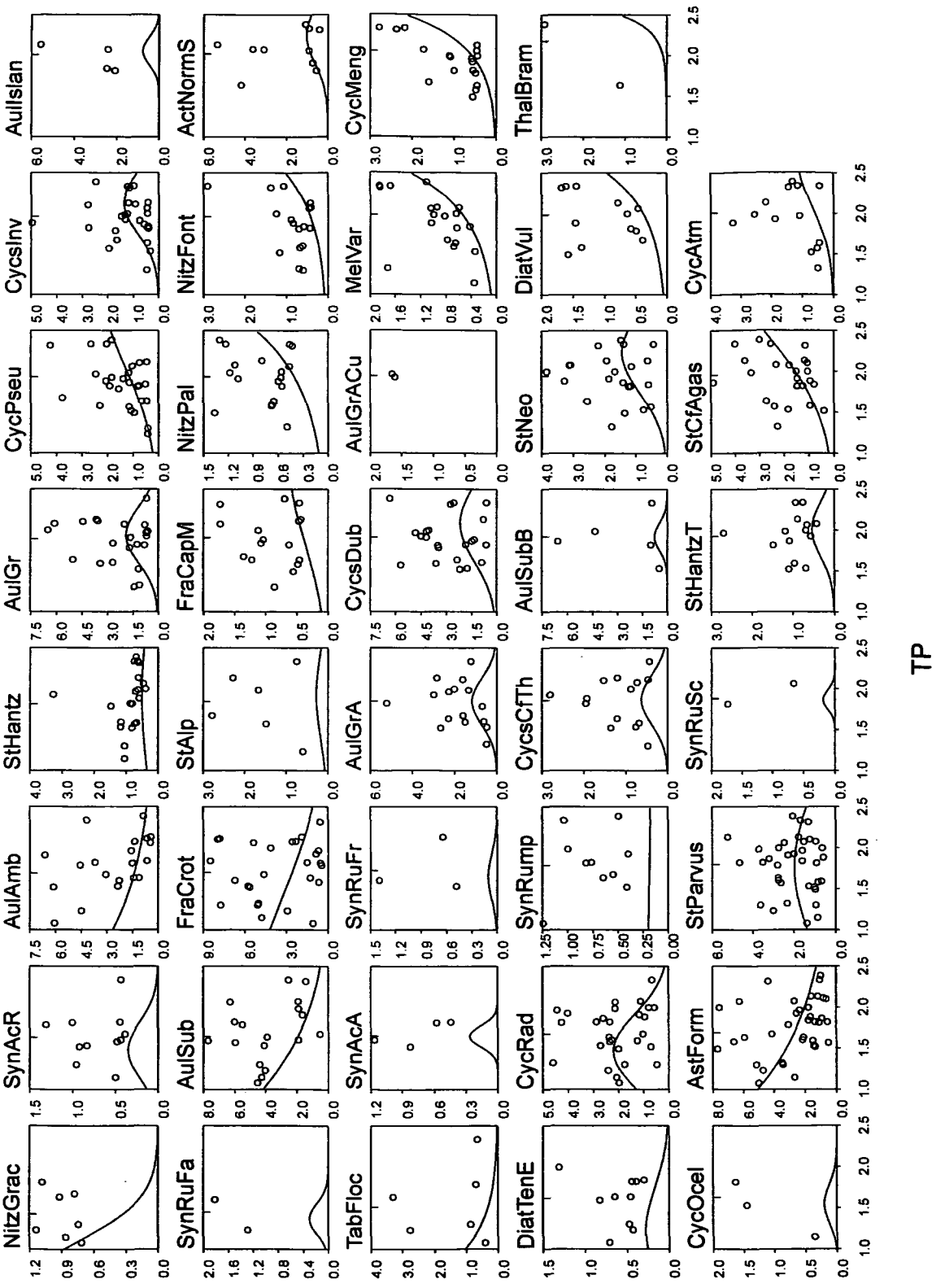


Figure 7.5b **Plots illustrating square-root transformed diatom species percentage relative abundance ($\sqrt{\ }$ %) against annual mean TP concentration (log_{10} μgl^{-1} TP) for the plankton-only dataset (40 sites and 39 species). Tick marks show the estimated WA TP optima for each species and the curves show the modelled response under logistic regression (LOGIT) (predicted unimodal fit). Species are ordered from low to high TP optima.**

Approximately a quarter of the species in the full dataset species and approximately one seventh in the plankton-only dataset exhibit no clear trend to TP concentrations. Species classified as showing no clear trend in relation to the TP gradient include the planktonic taxa *Synedra rumpens*, *Stephanodiscus parvus*, *Stephanodiscus alpinus* and *Stephanodiscus hantzschii*, and the periphytic taxa *Gyrosigma acuminatum*, *Amphora libyca*, *Navicula capitatoradiata*, *Fragilaria vaucheriae* and *Navicula gregaria*. As mentioned above, this may indicate that these species are responding to environmental variables other than TP and/or are highly tolerant to TP across a broad gradient or are cosmopolitan taxa. Again, this raises issues concerning the likely predictive ability of a TP inference model comprising species unresponsive to the environmental variable under reconstruction. This would be a particular problem if species showing no clear response to TP also have high effective abundance and therefore weight in core sequences (e.g. Hill's N^2 for *S. parvus* ~28, *A. minutissima* ~28, *F. vaucheriae* ~25, *A. libyca* ~22 and *S. hantzschii* ~15).

7.4.6 Comparative performance of DI-TP inference models created for UK lowland reservoirs with other published DI-TP models.

In this study, the best performing DI-TP model developed for UK lowland reservoirs using the full screened dataset (82 species and 41 sites) was the WAPLS (2) model (Table 7.3 and Figure 7.2b). For the plankton-only screened dataset (38 species from 39 sites), the model created using WA inverse deshrinking produced the most statistically robust model (Table 7.3 and Figures 7.3).

Table 7.6 presents the performance statistics of DI-TP inference models created in this study alongside those published in the literature. It can be seen from Table 7.6 that WAPLS models and internal validation of model predictive ability through the use of jack-knifing techniques were only developed and applied from 1996 onwards. This leads to difficulties in comparing and contrasting performance statistics between the earlier and later models. Authors also apply different transformations to both environmental variables and species datasets. In addition, meaningful comparisons between models are further complicated because authors rarely state all model statistics in published papers. However, the models created in this study are considered to perform at least as well as those listed in Table 7.6, in terms of both performance and predictive ability. This suggests that the UK lowland reservoir calibration set develops DI-TP inference models as robust and reliable as published models for other lake types and regions. However, this does not imply anything about the ecological relevance of applying DI-TP inference models generally. This will be discussed in sections 7.7 and Chapter 8.

Author	Area	No. of samples	Range (μgl^{-1})	Method	r^2 app. (boot)[1] (jack)[2]	app. RMSE (log μgl^{-1}) ($RMSE_{boot}$)[1] ($RMSEP_{jack}$)[2]	Trans-formation
Burgess (current study)	England (lowland reservoirs)	41 41 39 plank	12-242 12-242 12-242	WAPLS 2-component WA, inverse deshrinking WA, inverse deshrinking	0.87 (0.56)[2] 0.73 (0.53)[2] 0.68 (0.51)[2]	0.13 (0.23)[2] 0.18 (0.23)[2] 0.19 (0.24)[2]	log *x* TP √ species log *x* TP √ species log *x* TP √ species
Tibby (2004)	S.E. Australia (reservoirs)	33	7-451	WAPLS 2-component	0.94 (0.69)[2]	0.11 (0.25)[2]	ln(*x*+1) TP
Ramstack *et al.* (2003)	Minnesota, USA (lakes)	55	7-139	WA, inverse deshrinking	0.68	0.19 (0.25)[2]	log *x* TP
Philibert & Prairie (2002a)	Quebec, Canada (lakes)	72	3-52	WAPLS 2-component	0.89 (0.51)[2]	0.18 (0.50)[2]	log *x* TP
Bradshaw *et al.* (2002)	Denmark (shallow lakes)	29 29 plank	24–1145 24-1145	WAPLS 2-component WA_{tol}, classical deshrinking	0.86 (0.37)[2] 0.62 (0.23)[2]	0.13 (0.28)[2] 0.28 (0.32)[2]	log *x* TP log *x* TP
Kauppila *et al.* (2002)	S. Finland (lakes)	61	3-89	WAPLS 1-component	(0.76)[2]	(0.16)[2]	log *x* TP
Bradshaw & Anderson (2001)	Sweden (lakes)	43	7-369	WA_{tol} inverse deshrinking	0.75 (0.47)[2]	0.17 (0.24)[2]	log *x* TP
Reavie & Smol (2001)	S.E. Ontario Canada	45	4-540	WA, classical deshrinking	0.64 (0.47)[1]	0.007 * (0.01)[1] *	None TP √ species
King *et al.* (2000)	Lake District, UK	51 from 17 lakes	1-49	WA_{tol} classical deshrinking	0.64 (0.47)[2]	0.5 (0.58)[2]	ln(*x*+1) TP
Dixit *et al.* (1999)	N.E. USA	238	-	WA, classical deshrinking	0.55	(0.79)[1]	ln(*x*+1) TP
Gregory-Eaves *et al.* (1999)	Alaska, USA	51	3-83	WA, classical deshrinking	0.77 (0.52)[1]	0.16 (0.23)[1]	log *x* TP √ species
Lotter *et al.* (1998)	Alps, Europe	72	6-520	WAPLS 2-component	0.93	0.11 (0.19)[2]	log *x* TP
Bennion *et al.* (1996)	N.W. Europe	152	5-1190	WAPLS 2-component	0.91	0.15 (0.21)[2]	log *x* TP
Hall & Smol (1996)	South-central Ontario (Canada)	54	3-24	WA, classical deshrinking	0.62 (0.41)[1]	3.5 * (4.2)[1] *	None
Reavie *et al* (1995)	British Columbia, Canada	59	5-85	WA, classical deshrinking	0.73	0.33 (0.48)[1]	ln(*x*+1) TP √ species
Wunsam & Schmidt (1995)	Alps and pre-alpine region	86	2-266	$WA_{(tol)}$, classical deshrinking	0.57	0.32 (0.35)[1]	log *x* TP
Bennion (1993/1994)	S.E. England shallow lakes	30	25-646	WA, inverse deshrinking	0.79	0.16 (0.28)[1]	log *x* TP
Anderson & Rippey (1994)	Northern Ireland	49	15-800	WA classical deshrinking	0.8	0.19 (0.24)[1]	
Dixit & Smol (1994)	N.E. USA	64	1-154	WA classical deshrinking	0.62	0.66	ln(*x*+1) TP
Anderson *et al.* (1993)	Northern Ireland	43	25-800	WA inverse deshrinking	0.75	0.17	log *x* TP
Fritz *et al.* (1993b)	Michigan, USA	41	1-51	WA	0.73	0.41	ln(*x*+1) TP
Hall & Smol (1992)	British Columbia, Canada	37	5-28	WA, classical deshrinking	0.74	0.25	ln(*x*+1) TP

* RMSE and RMSEP in μgl^{-1}

Table 7.6 Comparison of the performance of DI-TP inference models created in this study with those published in the literature

There appears to be a contrast in terms of overall TP range between the models created from North American sites and those developed from European and Australian datasets. The former have TP ranges which are generally in the range 1-100 μgl^{-1} TP, and the latter have TP concentrations that in some sites exceed 1000 μgl^{-1}. However, this does not appear to be

associated with any particular distinction between different continents, but rather the idiosyncrasies of bedrock geologies and lake typologies of the specific regions selected for dataset development within each continent. This is exemplified in the European datasets by the low ranges and means of 1-49 μgl^{-1} (mean = 15) for the English Lake District (King *et al.*, 2000) and 2-266 μgl^{-1} (mean = 22) for the Alps and pre-Alps region (Wunsum & Schmidt, 1995). In contrast, the shallow lake datasets from Denmark (Bradshaw *et al.*, 2002) and S.E. England (Bennion, 1994) have much broader TP ranges, with higher mean values (164 and 104 respectively). The reservoir datasets presented in this study are most comparable, both in terms of TP range and performance statistics, with those presented by Bradshaw & Anderson (2001) for Swedish lakes and Tibby (2004) for S.E. Australian reservoirs. However the UK lowland reservoirs dataset spans a shorter TP gradient and includes fewer low TP sites than either of the aforementioned datasets. This may influence the definition of species' optima, possibly resulting in overestimation of TP optima for species whose growth preferences are for lower TP environments. A comparison of species optima derived from different calibration datasets will be considered in more detail in Chapter 9.

7.5 Development of DI-Chla inference models for UK lowland reservoirs

The development of preliminary DI-Chla inference models using all WA and WAPLS methods (see Figures 7.6a-c for selected examples) illustrated that there were no clear outliers (i.e. with residuals greater than the standard deviation of Chla) in either the full or plankton-only datasets. Therefore models were created using both the full (83 species and 42 sites) and plankton-only (39 species and 40 sites) datasets.

7.5.1 Comparative performance of the different DI-Chla models

Table 7.7 and Figures 7.6a-c illustrate that the WA inverse deshrinking model yielded the best performance statistics for both the full and plankton-only datasets. The full dataset gives jack-knifed error statistics of r^2_{jack} = 0.45, RMSEP = 0.20 $\log_{10}$ μgl^{-1}, mean bias = 0.004 $\log_{10}$ μgl^{-1} and maximum bias = 0.268 $\log_{10}$ μgl^{-1}. The plankton-only dataset yielded slightly less robust models although performance statistics are highly comparable, showing jack-knifed error statistics of r^2_{jack} = 0.37, RMSEP = 0.21 $\log_{10}$ μgl^{-1}, mean bias = -0.001 $\log_{10}$ μgl^{-1} and maximum bias = 0.265 $\log_{10}$ μgl^{-1}.

Species	model	deshrinking method	r^2	r^2 jack	RMSE apparent (log_{10} µg l^{-1})	RMSEP jack (log_{10} µgl^{-1})	mean bias (jack) (log_{10} µgl^{-1})	maximum bias (jack) (log_{10} µgl^{-1})
All	WA	classical	0.73	0.47	0.16	0.21	0.004	0.255
	WA	inverse	0.73	0.45	0.14	0.20	0.004	0.268
	WA_{tol}	classical	0.69	0.29	0.18	0.23	-0.019	0.406
	WA_{tol}	inverse	0.69	0.27	0.15	0.23	-0.014	0.429
	WAPLS (2)	-	0.83	0.45	0.11	0.21	-0.003	0.559
Plankton	WA	classical	0.67	0.38	0.19	0.23	-0.002	0.523
	WA	inverse	0.67	0.37	0.15	0.21	-0.001	0.265
	WA_{tol}	classical	0.69	0.24	0.18	0.25	-0.007	0.211
	WA_{tol}	inverse	0.69	0.22	0.15	0.24	-0.005	0.271
	WAPLS (2)	-	0.76	0.33	0.13	0.25	-0.026	0.746

Table 7.7 **Performance of the different DI-Chla models constructed using both the full (83 species, 42 site) and plankton-only (39 species, 40 sites) datasets. The best performing models are shaded.**

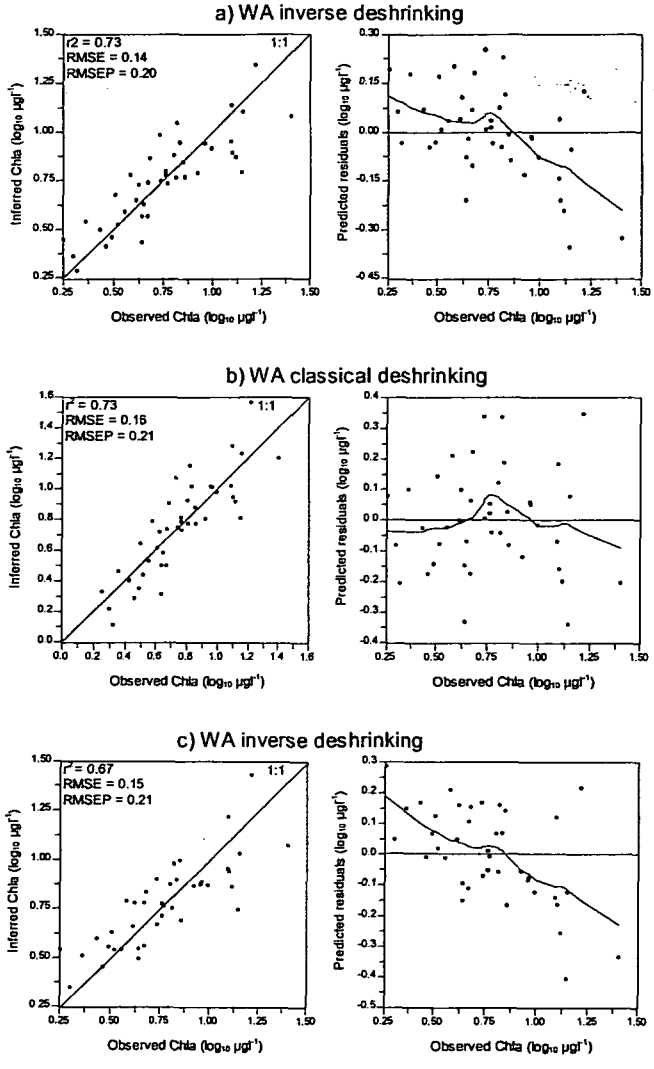


Figure 7.6a-c **Plots illustrating observed vs. inferred and observed vs. residual annual mean Chla (log_{10} µgl^{-1}) for the full dataset (7.6a-b) and the plankton-only dataset (7.6c). Only plots for the best performing models are shown.**

Although WA classical deshrinking produced models for both datasets that were not the best in terms of performance statistics, the pattern in the residuals across the full range of Chla shows a reduced trend. This reduction in model bias under classical deshrinking is similar to that seen in the DI-TP models (section 7.4.3) and similar to that reported by other authors (Hall & Smol, 1992; Anderson *et al.*, 1993; Bennion *et al.*, 1996).

7.5.2 Distributions, optima and tolerances of diatom species in the full and plankton-only datasets

Table 7.8 details the Chla optima and tolerances of the diatom species included in both the full and plankton-only datasets. Figure 7.7 illustrates the optima and tolerances of the full dataset taxa only, since in general, the optima and tolerances of the planktonic taxa in the plankton-only dataset are similar. Where there is a difference between the optima, the plankton-only model always produces higher optima. Only five species display a discrepancy of >0.25 μgl^{-1} Chla between the full and plankton-only datasets (*S. hantzschii* fo. *tenuis* (1.18), *D. tenuis* var. *elongatum* (0.37), *C. invisitatus* (0.35), *C.* cf. *tholiformis* (0.31), *F. capucina* var. *mesolepta* (0.29). The particularly high increase in Chla optima for *S. hantzschii* fo. *tenuis* in the plankton-only dataset probably arises because the site (Costessey) with a high relative abundance of this species in its surface sediments (~24%) has a relatively low Chla concentration in comparison to other sites where *S. hantzschii* fo. *tenuis* occurs. The comparatively low Chla concentration in Costessey's water may arise because the site receives water pumped directly from the River Wensum, which has only a very short residence time in the reservoir itself (~1 week), insufficient for the establishment of high in-lake algal populations and the generation of correspondingly high Chla concentrations. As a result, removal of Costessey in the plankton-only dataset leads to a significant increase in the WA optima of *S. hantzschii* fo. *tenuis*. Increases in the optima of other species are likely to arise for similar reasons. As noted for the DI-TP models created in section 7.4, caution should be exercised in the application of models and ensuing interpretation of results from sites where *S. hantzschii* fo. *tenuis* and other such species feature prominently in the sediment record. However, these discrepancies are relatively small and should be taken in the context of the overall differences in optima revealed between datasets in similar studies (as illustrated in relation to TP in Chapter 9).

Table 7.8 and Figure 7.7 show that species with high Chla optima (>7 μgl^{-1}) include the planktonic taxa *A. subarctica* fo. *subborealis*, *A. islandica*, *Synedra rumpens* var. *scotica*, *A. granulata*, *S. acus* var. *angustissima*, *A. granulata* var. *angustissima* fo. *curvata*, *C. ocellata*, *S. acus* var. *radians* and *S. hantzschii* fo. *tenuis*, and the periphytic taxa *Surirella*

Taxon code	n	n	Max %	Max %	Hill's N2	Hill's N2	Chla optima A	Chla optima B	Chla optima A	Chla optima B	Tolerance A	Tolerance C	Tolerance D	Tolerance A	Tolerance C	Tolerance D
AchLan	25		1.48		21.29		0.681	4.80			0.243	2.06	3.60			
AchMin	37		2.45		29.34		0.690	4.90			0.266	2.25	4.14			
ActNormS	10	10	5.35	5.35	6.05	6.05	0.672	4.70	0.672	4.70	0.150	1.37	1.94	0.150	1.37	1.94
AmphInar	11		1.23		9.28		0.788	6.13			0.244	2.63	4.64			
AmphLib	27		1.30		23.05		0.758	5.73			0.287	2.77	5.36			
AmphPed	25		2.00		20.38		0.710	5.13			0.275	2.41	4.53			
AstForm	38	36	7.71	7.71	24.98	23.66	0.671	4.68	0.689	4.89	0.241	1.99	3.49	0.234	2.04	3.49
AulAmb	21	20	6.65	6.65	13.13	12.92	0.747	5.58	0.750	5.63	0.269	2.57	4.80	0.267	2.59	4.77
AulGr	22	22	6.50	6.50	14.22	14.22	0.919	8.30	0.919	8.30	0.184	2.87	4.38	0.184	2.87	4.38
AulGrA	18	16	5.21	5.21	12.20	11.48	0.789	6.15	0.798	6.29	0.273	2.87	5.39	0.271	2.93	5.43
AulGrACu	2	2	1.65	1.65	2.00	2.00	0.900	7.94	0.900	7.94	0.134	2.11	2.87	0.134	2.11	2.87
AulIslan	4	4	5.57	5.57	3.33	3.33	0.973	9.40	0.973	9.40	0.186	3.28	5.02	0.186	3.28	5.02
AulSub	19	18	7.71	7.71	14.46	14.28	0.758	5.73	0.761	5.77	0.270	2.65	4.94	0.268	2.66	4.92
AulSubB	5	5	6.55	6.55	2.77	2.77	1.201	15.87	1.201	15.87	0.316	8.20	17.02	0.316	8.20	17.02
CocPed	17		1.64		14.33		0.612	4.10			0.261	1.86	3.36			
CocPlac	37		3.30		24.27		0.644	4.41			0.263	2.01	3.66			
CycAtm	13	13	3.28	3.28	9.20	9.20	0.737	5.46	0.737	5.46	0.355	3.05	6.90	0.355	3.05	6.90
CycMeng	20	18	2.79	2.79	13.58	12.08	0.668	4.66	0.677	4.76	0.321	2.44	5.09	0.334	2.56	5.50
CycOcel	3	3	1.64	1.64	2.41	2.41	0.898	7.91	0.898	7.91	0.244	3.40	5.96	0.244	3.40	5.96
CycPseu	28	27	4.25	4.25	19.81	18.92	0.713	5.17	0.715	5.19	0.287	2.50	4.83	0.292	2.54	4.97
CycRad	29	28	4.61	4.61	21.75	21.37	0.811	6.47	0.813	6.50	0.264	2.95	5.42	0.265	2.97	5.47
CycsCfTh	16	14	2.81	2.81	11.82	10.59	0.808	6.42	0.828	6.73	0.249	2.80	4.98	0.242	2.88	5.02
CycsDub	24	22	6.33	6.33	17.32	16.68	0.813	6.50	0.821	6.62	0.280	3.09	5.89	0.277	3.12	5.91
CycsInv	29	27	4.97	4.97	18.13	16.55	0.761	5.77	0.787	6.12	0.294	2.84	5.58	0.298	3.04	6.04
CymMic	8		1.08		7.35		0.697	4.98			0.249	2.18	3.85			
CymSin	2		1.23		1.83		0.316	2.07			0.125	0.52	0.69			
DenKuet	3		1.58		2.01		0.634	4.30			0.143	1.20	1.68			
DiatTenE	11	10	1.31	1.31	9.14	8.19	0.810	6.45	0.834	6.82	0.252	2.84	5.09	0.263	3.10	5.68
DiatVul	13	12	1.68	1.68	10.77	9.78	0.499	3.16	0.519	3.30	0.231	1.31	2.21	0.236	1.38	2.39
DipPar	17		1.97		13.43		0.701	5.02			0.194	1.81	2.83			
EncyCaes	4		1.03		3.84		0.566	3.68			0.310	1.88	3.84			
EncySil	29		1.60		23.71		0.693	4.93			0.315	2.54	5.26			
FraBrev	15		3.44		11.56		0.785	6.10			0.228	2.49	4.20			
FraCapM	17	16	1.73	1.73	13.98	12.98	0.660	4.57	0.687	4.86	0.259	2.05	3.73	0.249	2.12	3.77
FraConB	6		1.53		4.48		0.776	5.97			0.136	1.61	2.20			
FraCrot	26	26	8.51	8.51	17.35	17.35	0.823	6.66	0.823	6.66	0.183	2.30	3.48	0.183	2.30	3.48
FraEllip	10		2.32		8.66		0.863	7.30			0.222	2.93	4.86			
FraPinn	5		1.92		3.79		0.833	6.81			0.140	1.88	2.59			
FraVau	32		2.49		26.04		0.697	4.97			0.256	2.21	4.00			
GomAng	2		1.13		1.73		0.410	2.57			0.205	0.97	1.55			
GomMint	11		1.48		9.19		0.687	4.86			0.232	2.01	3.44			
GomOli	7		1.46		5.67		0.557	3.61			0.245	1.56	2.73			
GomOliM	6		1.52		4.77		0.593	3.91			0.238	1.65	2.87			
GomPar	26		1.08		23.79		0.678	4.76			0.269	2.20	4.09			
GomPum	2		1.23		1.65		0.651	4.47			0.007	0.06	0.08			
GyroAcc	33		1.68		28.35		0.768	5.86			0.261	2.65	4.83			
MelVar	21	19	1.85	1.85	16.91	15.21	0.639	4.36	0.655	4.52	0.284	2.10	4.02	0.286	2.18	4.21
NavCap	9		1.09		7.97		0.847	7.02			0.193	2.51	3.95			
NavCapr	25		1.25		22.14		0.741	5.51			0.283	2.64	5.06			
NavCari	9		1.12		8.06		0.710	5.12			0.336	2.75	6.00			
NavCrypt	18		1.47		15.61		0.676	4.75			0.311	2.43	4.96			
NavExil	4		1.67		3.62		0.591	3.90			0.405	2.37	6.01			
NavGreg	28		2.30		23.36		0.667	4.64			0.311	2.37	4.87			
NavLanc	22		2.58		15.89		0.569	3.71			0.272	1.73	3.22			
NavMen	30		1.12		27.80		0.707	5.09			0.274	2.38	4.48			
NavPslan	6		2.22		4.67		0.681	4.80			0.251	2.11	3.75			
NavPup	13		0.98		12.23		0.743	5.53			0.254	2.45	4.40			
NavTrip	12		1.40		10.43		0.633	4.30			0.365	2.45	5.65			
NavVen	17		1.41		14.10		0.664	4.61			0.203	1.72	2.75			
NitzAmp	10		1.07		8.89		0.798	6.28			0.350	3.48	7.78			
NitzDis	25		1.27		21.79		0.679	4.77			0.303	2.39	4.82			
NitzFont	19	17	2.90	2.90	13.50	12.00	0.692	4.92	0.709	5.12	0.291	2.40	4.70	0.292	2.51	4.90
NitzGrac	7	7	1.14	1.14	6.80	6.80	0.681	4.80	0.681	4.80	0.253	2.12	3.79	0.253	2.12	3.79
NitzPal	20	19	1.37	1.37	17.42	16.43	0.683	4.82	0.685	4.84	0.316	2.49	5.16	0.326	2.55	5.42
NitzRec	27		1.04		24.15		0.746	5.58			0.276	2.63	4.94			
NitzSinT	3		1.87		2.46		0.734	5.42			0.064	0.74	0.86			
RhAbbrev	29		3.03		20.60		0.691	4.90			0.302	2.45	4.94			
StAlp	6	6	2.79	2.79	4.86	4.86	0.709	5.12	0.709	5.12	0.379	2.98	7.13	0.379	2.98	7.13
StCfAgas	25	25	4.89	4.89	19.11	19.11	0.790	6.16	0.790	6.16	0.329	3.27	6.99	0.329	3.27	6.99
StHantz	22	21	3.28	3.28	15.85	14.94	0.827	6.71	0.842	6.95	0.261	3.03	5.54	0.267	3.19	5.90

Taxon code	n	n	Max %	Max %	Hill's N2	Hill's N2	Chla optima A	Chla optima B	Chla optima A	Chla optima B	Tolerance A	Tolerance C	Tolerance D	Tolerance A	Tolerance C	Tolerance D
StHantzT	15	14	4.93	2.70	8.49	10.87	0.846	7.02	0.914	8.20	0.290	3.42	6.66	0.301	4.10	8.21
StNeo	22	22	3.84	3.84	16.87	16.87	0.710	5.13	0.710	5.13	0.237	2.16	3.72	0.237	2.16	3.72
StParvus	37	36	5.25	5.25	27.99	27.37	0.839	6.91	0.847	7.03	0.287	3.35	6.46	0.282	3.36	6.43
SurBreb	11		0.97		10.00		0.551	3.56			0.265	1.63	2.99			
SurMin	12		1.00		10.70		0.877	7.53			0.355	4.20	9.53			
SynAcA	4	4	1.17	1.17	3.53	3.53	0.901	7.95	0.901	7.95	0.216	3.11	5.14	0.216	3.11	5.14
SynAcR	11	11	1.31	1.31	9.31	9.31	0.872	7.45	0.872	7.45	0.253	3.29	5.89	0.253	3.29	5.89
SynRuFa	2	2	1.82	1.82	1.94	1.94	0.629	4.26	0.629	4.26	0.088	0.79	0.95	0.088	0.79	0.95
SynRuFr	4	3	1.39	1.39	3.29	2.46	0.650	4.47	0.649	4.46	0.086	0.81	0.98	0.103	0.94	1.19
SynRump	11	10	1.24	1.24	9.55	8.80	0.797	6.26	0.805	6.38	0.369	3.58	8.40	0.379	3.71	8.90
SynRuSc	2	2	1.74	1.74	1.66	1.66	0.964	9.20	0.964	9.20	0.332	4.92	10.57	0.332	4.92	10.57
TabFloc	6	6	3.29	3.29	3.72	3.72	0.548	3.53	0.548	3.53	0.269	1.63	3.03	0.269	1.63	3.03
ThalBram	2	2	2.93	2.93	1.67	1.67	0.655	4.52	0.655	4.52	0.107	0.99	1.26	0.107	0.99	1.26

Table 7.8 **Chla WA diatom species optima and tolerances calculated from the full (83 species, 42 sites) and plankton-only (39 species, 40 sites) datasets. Shaded columns indicate data for the plankton-only dataset. A = log_{10} transformed Chla (log_{10} μgl^{-1}); B, C and D = back-transformed Chla (log_{10} μgl^{-1}); C = lower tolerance when back-transformed, D = higher tolerance when back-transformed.**

minuta, *Fragilaria elliptica* and *N. capitata*. Species with low Chla optima (<4 μgl^{-1}) include the planktonic taxa *D. vulgaris* and *T. flocculosa*, and the periphytic taxa *C. sinuata*, *G. angustatum*, *S. brebissonii*, *G. olivaceum*, *E. caespitosum*, *N. lanceolata*, *Navicula exilis* and *G. olivaceum* var. *minutissimum*. It is interesting to note that only two of the ten species with the highest Chla optima are periphytic and only two of the ten species with the lowest Chla optima are planktonic. This is to be expected because the planktonic diatom species are contributing to the measured Chla concentration in the reservoir waters. This indicates that it may be more appropriate to include all species in Chla inference models because eliminating periphytic species removes those species at the lower end of the Chla gradient.

Figures 7.8a and b illustrate for a) the full dataset (42 sites and 83 species) and b) the plankton-only dataset (40 sites and 39 species), diatom species percentage relative abundance ($\sqrt{}$ %) against annual mean Chla concentration (log_{10} μgl^{-1} Chla). Table 7.9 summarises the distribution patterns displayed by different diatom species. Over one third of the species distributions can be classified as unimodal. Species illustrating this distribution pattern include the planktonic taxa *T. bramaputrae*, *A. normanii* fo. *subsalsa*, *S. neoastraea*, *C.* cf. *tholiformis*, *A. granulata*, *A. islandica*, *A. granulata* var. *angustissima* fo. *curvata*, *F. crotonensis*, *A. formosa*, *S. rumpens* var. *familiaris*, *Synedra rumpens* var. *fragilarioides*, *S. acus* var. *angustissima* and *S. acus* var. *radians*, and the periphytic taxa *Diploneis parma*, *Fragilaria bevistriata*, *Fragilaria construens* fo. *binodis*, *F. pinnata*, *Navicula veneta* and *N. capitata*.

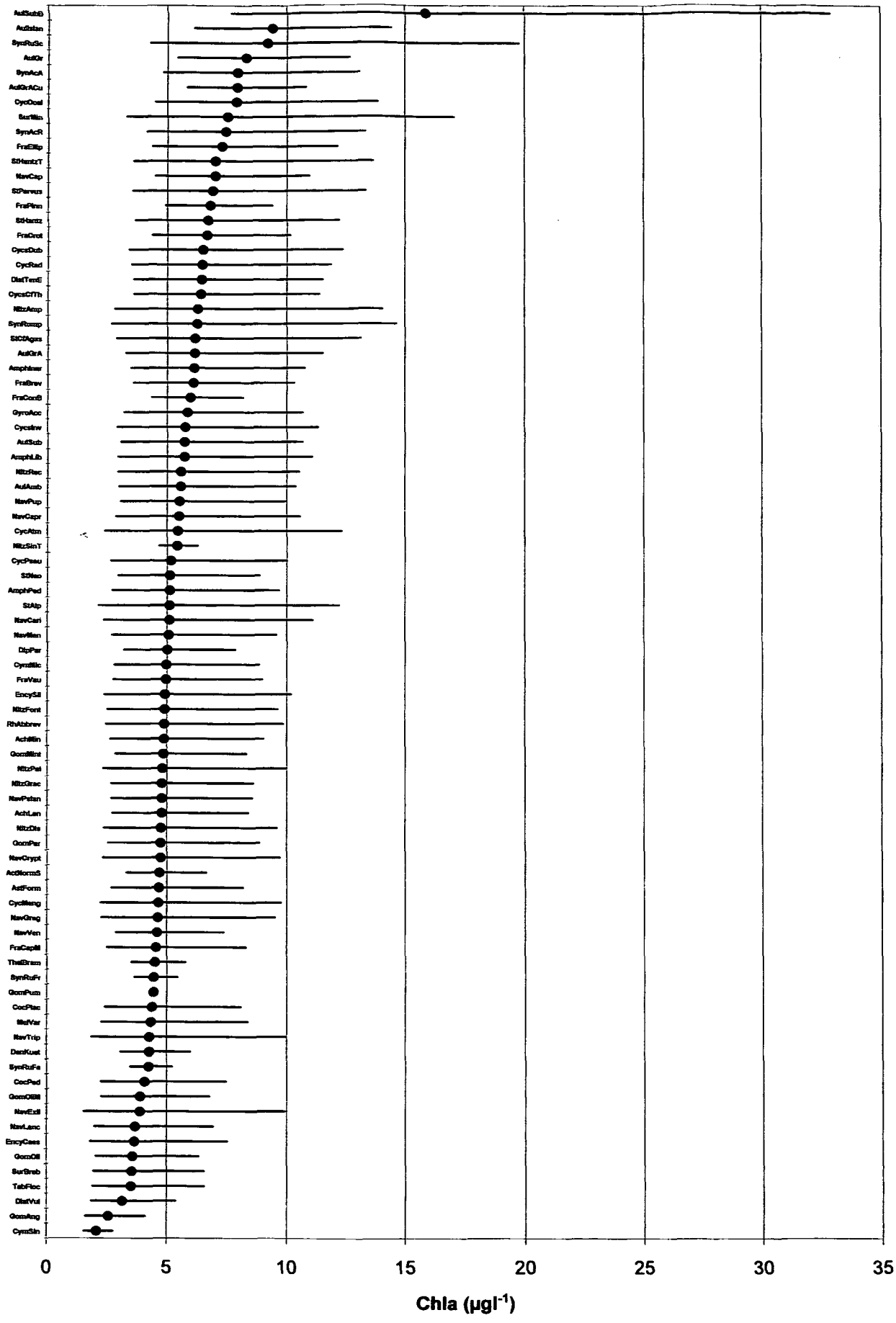


Figure 7.7 Chla optima and tolerances for the full dataset of 83 species and 42 sites.

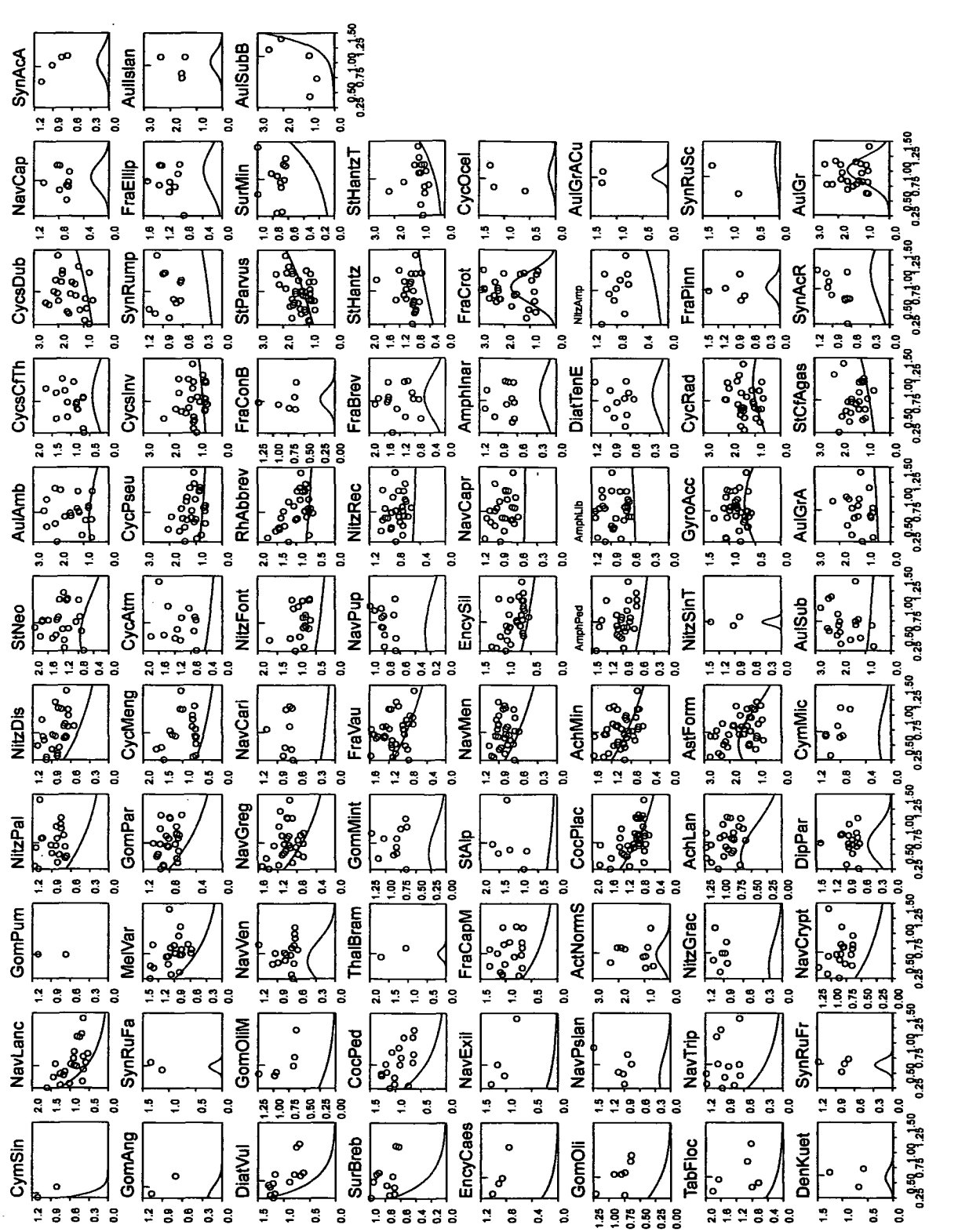


Figure 7.8a **Plots illustrating square-root transformed diatom species percentage relative abundance (√ %) against annual mean Chla concentration (log_{10} μgl^{-1} Chla) for the full dataset (42 sites and 83 species). Tick marks show the estimated species optima for each species and the curves are the modelled response under logistic regression (LOGIT) (predicted unimodal fit). Species are ordered according to Chla optima.**

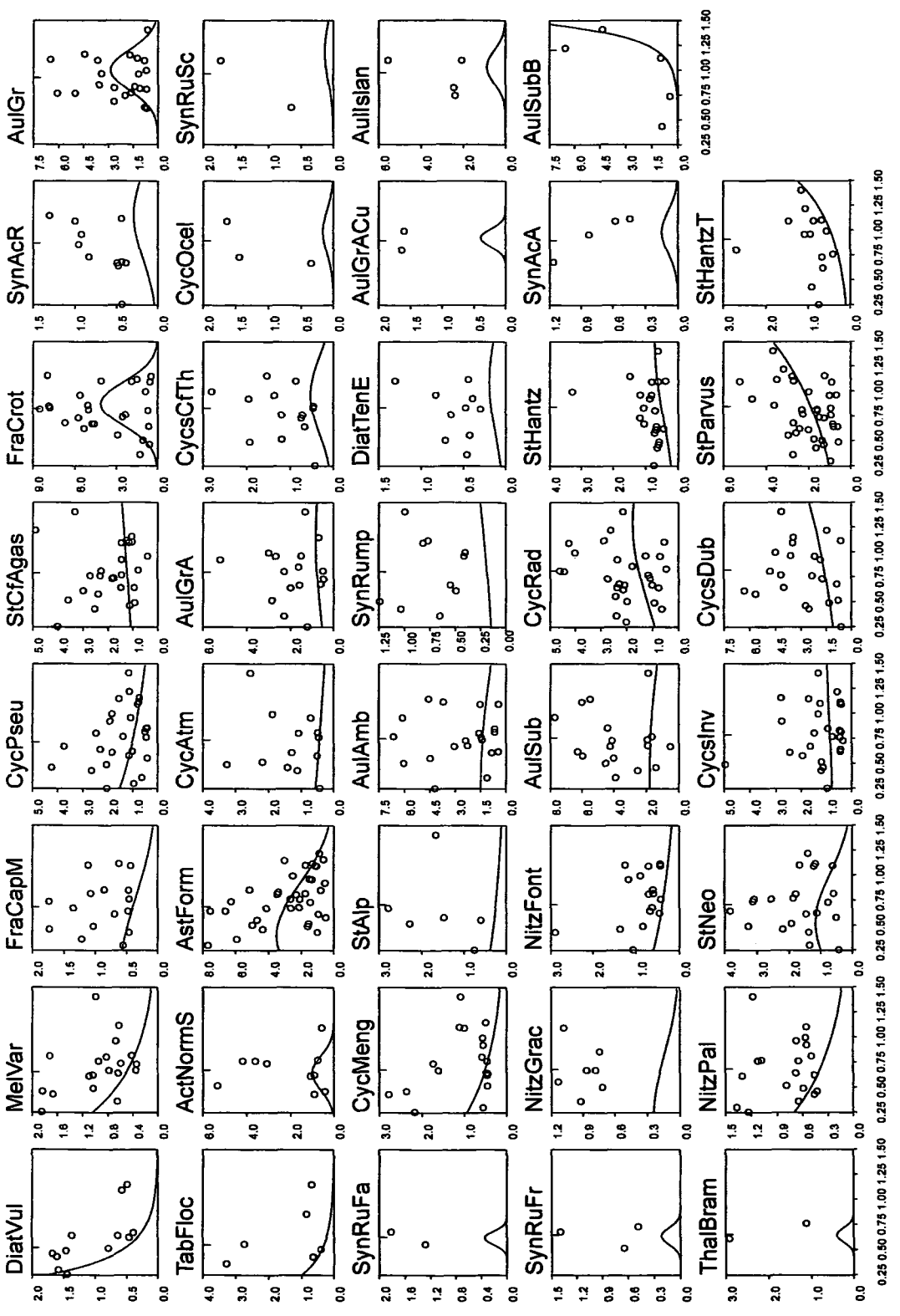


Figure 7.8b **Plots illustrating square-root transformed diatom species percentage relative abundance (√ %) against annual mean Chla concentration (log_{10} μgl^{-1} Chla) for the plankton-only dataset (40 sites and 39 species). Tick marks show the estimated species optima for each species and the curves are the modelled response under logistic regression (LOGIT) (predicted unimodal fit). Species are ordered according to Chla optima.**

More species distributions were truncated at the lower end (30%) than the upper end (5%) for the full dataset (21% and 8% respectively for the plankton-only dataset), in contrast to the pattern of truncations seen in the TP distributions. Species distributions truncated at the lower end indicate that the optima for these species are probably overestimated. Species showing this distribution include the planktonic taxa *T. flocculosa*, *F. capucina* var. *mesolepta*, *C. meneghiniana*, *D. vulgaris*, *M. varians*, *N. palea* and the periphytic taxa *Cocconeis placentula*, *C. pediculus*, *G. angustatum*, *Gomphonema parvulum*, *S. brebissonii*, *N. gregaria*, *N. lanceolata*, *N. cryptocephala*, *Navicula tripunctata*, *A. minutissima* and *C. sinuata*. Several of these species (e.g. *M. varians*, *N. gregaria*, *N. palea* and *G. parvulum*) occur in sites spanning a large portion of the Chla gradient. It is unclear whether their optima truly are overestimated or whether they have a broad tolerance for Chla. Furthermore, it should be recognised that their distributions could be largely determined by environmental variables other than Chla.

There were only a few species (<10% for both datasets) whose Chla distributions were truncated at the upper end of the Chla gradient, indicating that a wide Chla gradient has been sampled in this study. Species with possibly underestimated optima include the species *A. subarctica* fo. *subborealis*, *S. parvus*, *S. hantzschii* fo. *tenuis* and *S. minuta*. The optima of these species may be better defined if more sites with high Chla concentrations were included in the dataset, although it may not be possible to locate many more high Chla reservoirs in the UK. It is noted however that *A. subarctica* fo. *subborealis* was commonly found in turbid S.E. Australian reservoirs (Denys *et al.*, 2003; Tibby, 2004) and the combination of both this and the UK lowland reservoir calibration set may lead to a more clearly defined optimum for this species.

Species distribution	Full dataset		Plankton-only dataset	
	number	%	number	%
Unimodal	30	**36**	15	**38**
Truncated (lower end)	25	**30**	8	**21**
Truncated (upper end)	4	**5**	3	**8**
No clear trend	24	**29**	13	**33**

Table 7.9 Classification of diatom species distributions in relation to Chla for both the full and plankton-only datasets.

Approximately a third of the diatom species in both datasets exhibit no clear trend in response to Chla concentrations. Species with this classification include the planktonic taxa *A. subarctica*, *A. ambigua*, *A. granulata* var. *angustissima*, *C. radiosa*, *Cyclostephanos dubius*, *C. invisitatus*, *S. alpinus* and *S. hantzschii*, and the periphytic taxa *R. abbreviata*,

Gyrosigma acuminatum, *A. libyca*, *N. recta*, and *N. capitatoradiata*. This may indicate that these species are responding to environmental variables other than Chla and/or are highly tolerant to Chla across a broad gradient.

7.5.3 Comparative performance of DI-Chla inference models created in this study with those published in the literature.

There are few published DI-Chla models with which to compare the models created in this study. Unfortunately, the performance statistics of the model created by Jones & Juggins (1995) uses the cross-validation technique of bootstrapping and not jack-knifing as in this study (Table 7.10). This makes the process of model comparison more difficult. The apparent r^2 value of their model is highly comparable to that for the full model in this study (0.73 and 0.74 respectively), but their apparent RMSE is over double that generated by the full and plankton-only models in this study (0.32 compared with 0.14 and 0.15). This suggests that the predictive capability of DI-Chla models based on a calibration set of UK lowland reservoirs is greater than that of the model created for Antarctic lakes by Jones & Juggins (1995). This is probably because the Antarctic lakes have very little plankton and are dominated by benthic diatoms (Jones & Juggins, 1995). Conversely, the UK lowland reservoirs are dominated by planktonic diatoms, which are likely to better reflect epilimnetic Chla concentrations than benthic taxa. This is because benthic diatoms are probably responding to a more diverse range of environmental factors than planktonic taxa. The predictive ability of the models dominated by planktonic species in the present study are more robust, with better defined optima than those determined for Antarctic lakes dominated by benthic taxa.

Author	Area	No. of samples	Range (μgl^{-1})	Method	r^2 app. (boot)[1] (jack)[2]	app. RMSE (log μgl^{-1}) ($RMSE_{boot}$)[1] ($RMSEP_{jack}$)[2]	Trans-formation
Burgess (current study)	England (lowland reservoirs)	42	1.8 – 25.5	WA, inverse deshrinking	0.73 (0.45)[2]	0.14 (0.20)[2]	log x Chla √ species
		40 plank	1.8 – 25.5	WA, inverse deshrinking	0.67 (0.37)[2]	0.15 (0.21)[2]	log x Chla √ species
Jones & Juggins (1995)	Antarctic lakes	59	-	WA classical deshrinking	0.74	0.32 (0.38)[1]	log x TP

Table 7.10 Comparison of the performance of DI-Chla inference models created in this study with those published in the literature

7.6 Development of DI-EC inference models for UK lowland reservoirs.

The development of preliminary DI-EC inference models using all WA and WAPLS methods (see Figures 7.9a-d for selected examples) illustrated that there were no clear outliers (i.e. with residuals greater than the standard deviation of EC) in either the full or plankton-only datasets. Therefore models were created using both the full (83 species and 42 sites) and plankton-only (39 species and 40 sites) datasets.

7.6.1 Comparative performance of the different DI-EC models

Table 7.11 illustrates the results of preliminary DI-EC inference models developed from non-transformed EC data. Figure 7.9a shows that the EC data are inherently skewed, as discussed in section 7.3.1, and as such a considerable trend is demonstrated in the pattern of residuals. It is clear from Figures 7.9b-d that the relationship between observed and inferred EC is improved by $\log_{10}$ transforming the EC data. The model performance statistics presented in Tables 7.11 and 7.12 show that $\log_{10}$ transforming the EC data increases r^2_{jack} from 0.59 to 0.72 for the corresponding WA inverse deshrinking models for the full dataset.

species	model	deshrinking method	r^2	r^2 jack	RMSE apparent (μScm^{-1})	RMSEP jack (μScm^{-1})	mean bias (jack) (μScm^{-1})	maximum bias (jack) (μScm^{-1})
all	WA	classical	0.77	0.60	88.57	112.39	1.831	218.41
	WA	inverse	0.77	0.59	77.93	105.70	0.472	244.76
	WA_{tol}	classical	0.79	0.59	84.19	107.73	-10.666	223.07
	WA_{tol}	inverse	0.79	0.58	74.90	106.66	-9.589	247.07
	WAPLS (2)		0.85	0.46	63.32	125.14	-3.241	270.88
plankton	WA	classical	0.75	0.57	91.50	117.02	4.337	204.56
	WA	inverse	0.75	0.55	79.19	106.71	2.448	238.59
	WA_{tol}	classical	0.76	0.35	89.11	151.21	16.954	381.58
	WA_{tol}	inverse	0.76	0.36	77.62	131.56	11.410	333.30
	WAPLS (2)		0.81	0.47	69.25	119.56	-4.237	265.70

Table 7.11 No transformation of EC. Performance of the different DI-EC models based on both the full (83 species, 42 site) and the plankton-only (39 species, 40 site) datasets.

species	Model	deshrinking method	r^2	r^2 jack	RMSE apparent ($log10\ \mu Scm^{-1}$)	RMSEP jack ($log10\ \mu Scm^{-1}$)	mean bias (jack) ($log10\ \mu Scm^{-1}$)	maximum bias (jack) ($log10\ \mu Scm^{-1}$)
All	WA	classical	0.84	0.73	0.09	0.11	0.002	0.104
	WA	inverse	0.84	0.72	0.08	0.10	0.001	0.140
	WA_{tol}	classical	0.86	0.73	0.08	0.10	-0.019	0.135
	WA_{tol}	inverse	0.86	0.72	0.07	0.11	-0.018	0.164
	WAPLS (2)		0.89	0.66	0.07	0.12	-0.003	0.146
Plankton	WA	classical	0.79	0.67	0.10	0.12	0.006	0.077
	WA	inverse	0.79	0.65	0.09	0.11	0.004	0.155
	WA_{tol}	classical	0.83	0.51	0.09	0.15	0.009	0.272
	WA_{tol}	inverse	0.83	0.52	0.08	0.14	0.006	0.263
	WAPLS (2)		0.84	0.63	0.08	0.12	0.002	0.141

Table 7.12 After $\log_{10}$ transformation of EC. Performance of the different DI-EC models based on both the full (83 species, 42 site) and the plankton-only (39 species, 40 site) datasets. The best performing models are shaded.

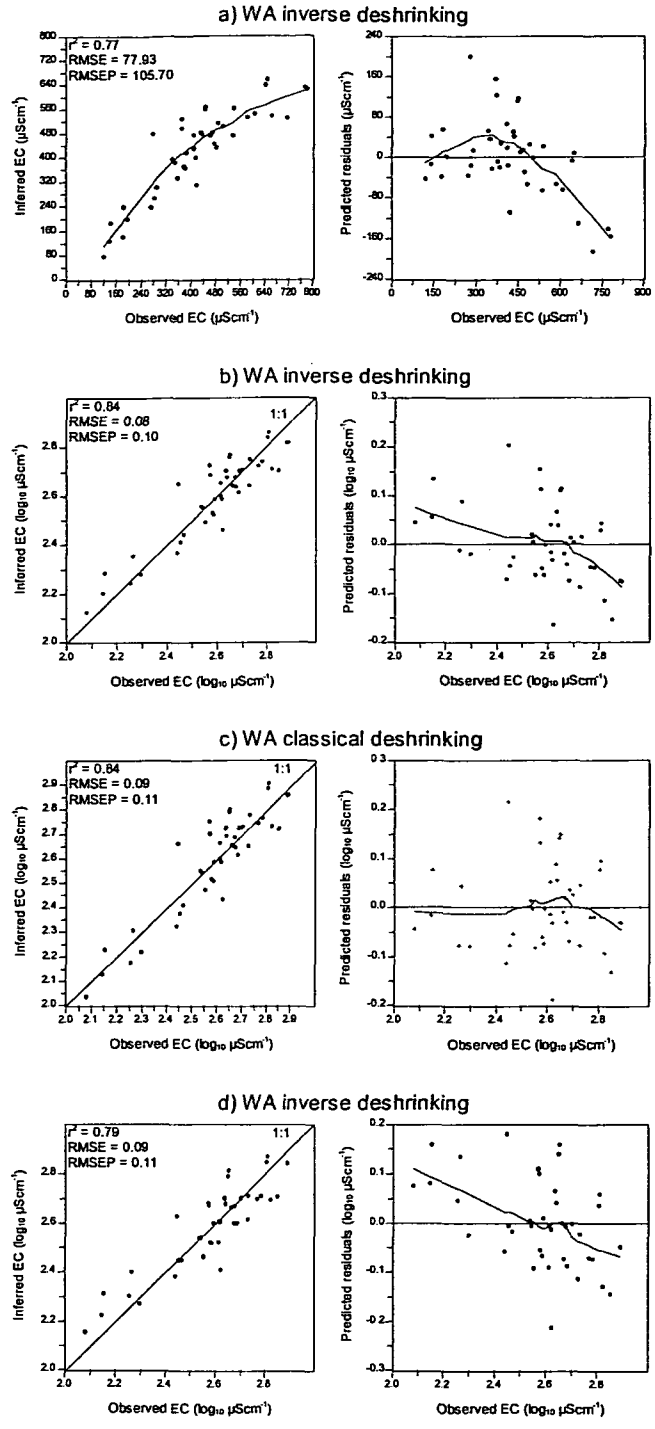


Figure 7.9a-d. **Plots illustrating observed vs. inferred and observed vs. residual annual mean EC (a: μScm^{-1}, b-d: log_{10} μScm^{-1}) for the full dataset (7.9a-c) and the plankton-only dataset (7.9d). Only plots for the best performing models are shown.**

Table 7.12 and Figures 7.9b-d illustrate that the WA inverse deshrinking model yielded the best performance statistics for both the full and plankton-only datasets. The full dataset shows jack-knifed error statistics of $r^2_{jack} = 0.72$, RMSEP = 0.10 log_{10} μScm^{-1}, mean bias = 0.001 log_{10} μScm^{-1} and maximum bias = 0.140 log_{10} μScm^{-1}. The plankton-only dataset yielded slightly less robust models although performance statistics are highly comparable, showing jack-knifed error statistics of $r^2_{jack} = 0.65$, RMSEP = 0.11 log_{10} μScm^{-1}, mean bias

= -0.004 $\log_{10}$ μScm^{-1} and maximum bias = 0.155 $\log_{10}$ μScm^{-1}. These results show that the DI-EC models produce better performance statistics than those developed for TP (Table 7.3) and Chla (Table 7.7), and these models should provide more accurate inferences when applied to sediment core sequences.

Although WA classical deshrinking produces models for both datasets that are not the best in terms of performance statistics, the pattern in the residuals across the full range of EC shows very little trend. This reduction in model bias under classical deshrinking is similar to that seen in both the DI-TP and DI-Chla models (sections 7.4.3 and 7.5.1).

7.6.2 Distributions, optima and tolerances of diatom species in the full and plankton-only datasets

Table 7.13 details the EC optima and tolerances of the diatom species included in both the full and plankton-only datasets and Figure 7.10 displays these optima and tolerance ranges for the full dataset only because the optima and tolerances are generally similar in both the full and plankton-only datasets. If the optima are different, the discrepancy is always expressed as a lower optima in the plankton-only dataset and there is rarely a discrepancy exceeding 20 μScm^{-1} EC. Exceptions include *S. hantzschii* fo. *tenuis* whose optimum decreases by 76 μScm^{-1}, from 464 to 388 μScm^{-1} EC. The reason for this decrease in optima is due to *S. hantzschii* fo. *tenuis* occurring at a high (~24%) relative abundance in Costessey. This site has a high conductivity and its elimination in the plankton-only dataset consequently reduces the EC optima of *S. hantzschii* fo. *tenuis* - a similar effect to that seen in section 7.5.2 for Chla and section 7.4.5 for TP. *S. hantzschii*, *S. rumpens* var. *fragilarioides*, *D. tenuis* var. *elongatum* and *C. invisitatus* also show significantly lower EC optima (20–57 μScm^{-1} lower) in the plankton-only dataset. These differences could partly determine the relative capabilities of the full and plankton-only DI-EC models to reliably reconstruct EC.

Species with high EC optima (>500 μScm^{-1}) include the planktonic species *A. normanii* fo. *subsalsa*, *T. bramaputrae*, *C. atomus* and *S. neoastraea*, and the periphytic taxa *G. pumilum*, *Navicula pseudolanceolata*, *G. olivaceum* var. *minutissimum*, *C. pediculus*, *N. tripunctata*, *Fragilaria elliptica* and *Amphora pediculus*. Species with low EC optima (<300 μScm^{-1}) include the planktonic species *T. flocculosa*, *S. rumpens* var. *familiaris*, *N. gracilis*, *A. subarctica*, *S. acus* var. *radians* and *A. ambigua*, and the periphytic species *D. kuetzingii* and *N. sinuata* var. *tabellaria*.

Taxon code	n	n	Max %	Max %	Hill's N2	Hill's N2	EC optima A	EC optima B	EC optima A	EC optima B	Tolerance A	Tolerance C	Tolerance D	Tolerance A	Tolerance C	Tolerance D
AchLan	25		1.48		21.29		2.614	411			0.197	150	236			
AchMin	37		2.45		29.34		2.560	363			0.220	144	240			
ActNormS	10	10	5.35	5.35	6.05	6.05	2.734	543	2.734	543	0.125	137	180	0.125	137	180
AmphInar	11		1.23		9.28		2.677	476			0.163	149	216			
AmphLib	27		1.30		23.05		2.677	476			0.159	146	209			
AmphPed	25		2.00		20.38		2.700	501			0.128	128	172			
AstForm	38	36	7.71	7.71	24.98	23.66	2.559	362	2.549	354	0.239	153	266	0.242	151	264
AulAmb	21	20	6.65	6.65	13.13	12.92	2.457	287	2.455	285	0.215	112	183	0.215	111	183
AulGr	22	22	6.50	6.50	14.22	14.22	2.650	447	2.650	447	0.142	125	172	0.142	125	172
AulGrA	18	16	5.21	5.21	12.20	11.48	2.636	433	2.631	427	0.182	149	225	0.181	145	222
AulGrACu	2	2	1.65	1.65	2.00	2.00	2.648	445	2.648	445	0.288	216	418	0.288	216	418
AulIsIan	4	4	5.57	5.57	3.33	3.33	2.676	474	2.676	474	0.038	39	44	0.038	39	44
AulSub	19	18	7.71	7.71	14.46	14.28	2.416	261	2.414	259	0.194	94	146	0.194	93	147
AulSubB	5	5	6.55	6.55	2.77	2.77	2.625	421	2.625	421	0.046	42	48	0.046	42	48
CocPed	17		1.64		14.33		2.721	527			0.117	125	162			
CocPlac	37		3.30		24.27		2.642	439			0.169	142	208			
CycAtm	13	13	3.28	3.28	9.20	9.20	2.711	514	2.711	514	0.133	136	184	0.133	136	184
CycMeng	20	18	2.79	2.79	13.58	12.08	2.671	469	2.655	452	0.136	126	172	0.128	115	155
CycOcel	3	3	1.64	1.64	2.41	2.41	2.544	350	2.544	350	0.191	125	193	0.191	125	193
CycPseu	28	27	4.25	4.25	19.81	18.92	2.625	422	2.616	413	0.165	134	195	0.160	127	184
CycRad	29	28	4.61	4.61	21.75	21.37	2.543	349	2.539	346	0.210	134	217	0.208	132	212
CycsCfTh	16	14	2.81	2.81	11.82	10.59	2.739	548	2.734	542	0.122	134	178	0.122	133	176
CycsDub	24	22	6.33	6.33	17.32	16.68	2.623	420	2.620	417	0.164	132	192	0.164	131	191
CycsInv	29	27	4.97	4.97	18.13	16.55	2.681	479	2.661	458	0.152	141	202	0.147	131	185
CymMic	8		1.08		7.35		2.585	385			0.188	136	208			
CymSin	2		1.23		1.83		2.571	372			0.001	0	1			
DenKuet	3		1.58		2.01		2.345	222			0.184	77	116			
DiatTenE	11	10	1.31	1.31	9.14	8.19	2.593	391	2.547	353	0.284	187	362	0.277	167	314
DiatVul	13	12	1.68	1.68	10.77	9.78	2.675	473	2.673	471	0.130	122	165	0.138	128	176
DipPar	17		1.97		13.43		2.553	357			0.183	123	188			
EncyCaes	4		1.03		3.84		2.687	486			0.109	108	139			
EncySil	29		1.60		23.71		2.595	394			0.196	143	224			
FraBrev	15		3.44		11.56		2.654	451			0.154	135	192			
FraCapM	17	16	1.73	1.73	13.98	12.98	2.632	429	2.628	425	0.183	148	224	0.189	150	231
FraConB	6		1.53		4.48		2.586	385			0.218	152	252			
FraCrot	26	26	8.51	8.51	17.35	17.35	2.538	345	2.538	345	0.183	119	181	0.183	119	181
FraEllip	10		2.32		8.66		2.707	510			0.120	124	161			
FraPinn	5		1.92		3.79		2.522	333			0.275	156	294			
FraVau	32		2.49		26.04		2.609	407			0.177	137	204			
GomAng	2		1.13		1.73		2.677	476			0.028	30	31			
GomMint	11		1.48		9.19		2.682	481			0.110	108	138			
GomOli	7		1.46		5.67		2.630	427			0.183	147	223			
GomOliM	6		1.52		4.77		2.739	548			0.119	131	173			
GomPar	26		1.08		23.79		2.561	364			0.207	138	222			
GomPum	2		1.23		1.65		2.871	744			0.046	76	82			
GyroAcc	33		1.68		28.35		2.624	421			0.164	133	193			
MelVar	21	19	1.85	1.85	16.91	15.21	2.620	416	2.607	405	0.136	111	154	0.132	106	143
NavCap	9		1.09		7.97		2.654	451			0.176	150	225			
NavCapr	25		1.25		22.14		2.651	448			0.158	137	196			
NavCari	9		1.12		8.06		2.618	415			0.138	113	155			
NavCrypt	18		1.47		15.61		2.637	433			0.182	148	226			
NavExil	4		1.67		3.62		2.681	480			0.075	76	90			
NavGreg	28		2.30		23.36		2.594	393			0.181	134	203			
NavLanc	22		2.58		15.89		2.655	452			0.172	148	219			
NavMen	30		1.12		27.80		2.640	436			0.157	132	191			
NavPslan	6		2.22		4.67		2.749	561			0.091	106	131			
NavPup	13		0.98		12.23		2.692	492			0.133	130	176			
NavTrip	12		1.40		10.43		2.717	521			0.105	112	143			
NavVen	17		1.41		14.10		2.617	414			0.230	170	289			
NitzAmp	10		1.07		8.89		2.692	492			0.109	109	140			
NitzDis	25		1.27		21.79		2.657	454			0.129	117	157			
NitzFont	19	17	2.90	2.90	13.50	12.00	2.644	440	2.632	429	0.152	130	185	0.150	126	176
NitzGrac	7	7	1.14	1.14	6.80	6.80	2.319	209	2.319	209	0.241	89	154	0.241	89	154
NitzPal	20	19	1.37	1.37	17.42	16.43	2.666	463	2.654	450	0.144	130	183	0.137	121	168
NitzRec	27		1.04		24.15		2.644	440			0.151	129	184			
NitzSinT	3		1.87		2.46		2.436	273			0.159	84	121			
RhAbbrev	29		3.03		20.60		2.672	470			0.132	123	167			
StAlp	6	6	2.79	2.79	4.86	4.86	2.607	405	2.607	405	0.191	144	223	0.191	144	223
StCfAgas	25	25	4.89	4.89	19.11	19.11	2.661	458	2.661	458	0.108	101	129	0.108	101	129
StHantz	22	21	3.28	3.28	15.85	14.94	2.626	423	2.603	401	0.200	156	247	0.191	143	221

Taxon code	*n*	*n*	Max %	Max %	Hill's N2	Hill's N2	EC optima A	EC optima B	EC optima A	EC optima B	Tolerance A	Tolerance C	Tolerance D	Tolerance A	Tolerance C	Tolerance D
StHantzT	15	14	4.93	2.70	8.49	10.87	2.667	464	2.589	388	0.173	152	228	0.117	92	120
StNeo	22	22	3.84	3.84	16.87	16.87	2.704	505	2.704	505	0.114	116	153	0.114	116	153
StParvus	37	36	5.25	5.25	27.99	27.37	2.556	359	2.554	358	0.208	136	222	0.209	137	221
SurBreb	11		0.97		10.00		2.668	466			0.096	93	115			
SurMin	12		1.00		10.70		2.597	395			0.149	114	162			
SynAcA	4	4	1.17	1.17	3.53	3.53	2.554	358	2.554	358	0.114	83	108	0.114	83	108
SynAcR	11	11	1.31	1.31	9.31	9.31	2.449	281	2.449	281	0.194	101	159	0.194	101	159
SynRuFa	2	2	1.82	1.82	1.94	1.94	2.290	195	2.290	195	0.255	87	156	0.255	87	156
SynRuFr	4	3	1.39	1.39	3.29	2.46	2.604	402	2.538	345	0.239	170	295	0.210	132	215
SynRump	11	10	1.24	1.24	9.55	8.80	2.544	350	2.525	335	0.228	143	242	0.218	132	218
SynRuSc	2	2	1.74	1.74	1.66	1.66	2.649	445	2.649	445	0.093	85	107	0.093	85	107
TabFloc	6	6	3.29	3.29	3.72	3.72	2.224	168	2.224	168	0.160	52	74	0.160	52	74
ThalBram	2	2	2.93	2.93	1.67	1.67	2.718	522	2.718	522	0.172	170	254	0.172	170	254

Table 7.13 EC WA diatom species optima and tolerances calculated from the full (83 species, 42 sites) and plankton-only (39 species, 40 sites) datasets. Shaded columns indicate data for the plankton-only dataset. A = log_{10} transformed EC (log_{10} μScm^{-1}); B, C and D = back-transformed EC (log_{10} μScm^{-1}); C = lower tolerance when back-transformed, D = higher tolerance when back-transformed.

Figures 7.11a-b illustrate square-root transformed diatom species percentage relative abundance data ($\sqrt{}$ %) against annual mean EC concentration (μScm^{-1}) for a) the full dataset (42 sites and 83 species) and b) the plankton-only dataset (40 sites and 39 species). Table 7.14 summarises the distribution patterns displayed by different diatom species. Approximately half the taxa show a unimodal distribution to EC in both the full and plankton-only datasets. Species frequently occurring in the datasets and showing a unimodal response to EC include the planktonic taxa *F. crotonensis*, *A. subarctica*, *A. granulata*, *M. varians*, *C. meneghiniana*, *Cyclotella pseudostelligera*, *C. invisitatus*, *S. neoastraea*, *S.* cf. *agassizensis* and *N. palea*, and the non-planktonic taxa *S. minuta*, *Navicula menisculus*, *R. abbreviata*, *N. dissipata*, *Gyrosigma acuminatum*, *C. pediculus* and *A. pediculus*.

Relatively few taxa show truncated distributions either at the upper (~10%) or lower (~10%) ends of the EC gradient. Species with truncated distributions at the upper end include *N. palea*, *T. bramaputrae*, *C.* cf. *tholiformis*, *A. normanii* fo. *subsalsa*, *N. lanceolata*, *N. cryptocephala* and *N. veneta*. Species with truncated distributions at the lower end include *T. flocculosa*, *A. ambigua*, *C. radiosa*, *D. parma* and *G. parvulum*.

Approximately a quarter to a third of species show no clear trend in response to EC. Species that are likely to be responding to environmental variables other than EC include the planktonic taxa *S. hantzschii*, *S. hantzschii* fo. *tenuis*, *S. parvus*, *S. alpinus*, *C. dubius* and *A. formosa*, and the periphytic taxa *N. capitata*, *A. minutissima*, *F. pinnata*, *F. vaucheriae* and *G. olivaceum*.

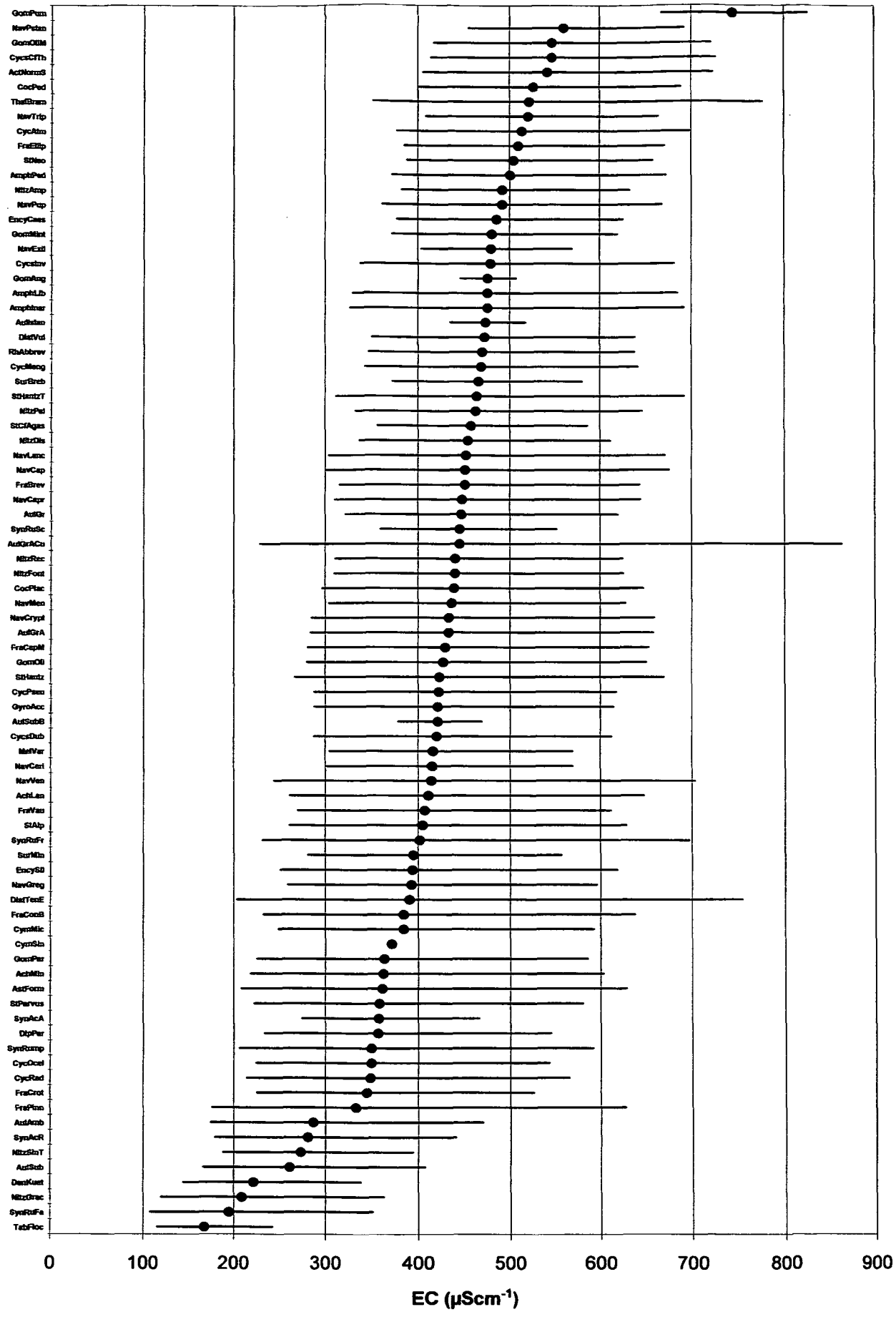


Figure 7.10 EC optima and tolerance ranges for diatom species in the full dataset (83 species, 42 sites).

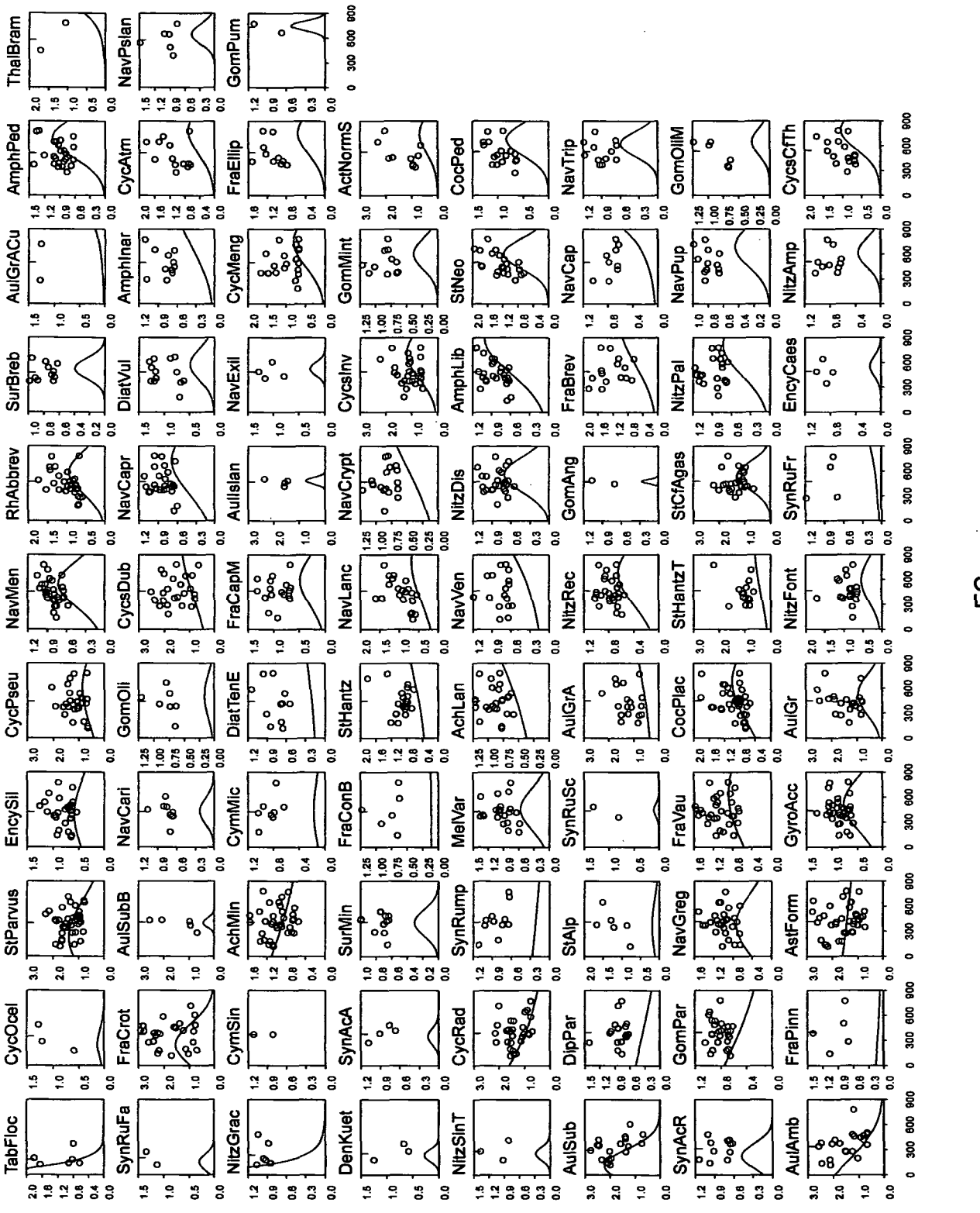


Figure 7.11a Plots illustrating square-root transformed diatom species percentage relative abundance (√ %) against annual mean EC concentration (log_{10} μScm^{-1} EC) for the full dataset (42 sites and 83 species). Tick marks show the estimated species optima for each species and the curves are the modelled response under logistic regression (LOGIT) (predicted unimodal fit). Species are ordered according to EC optima.

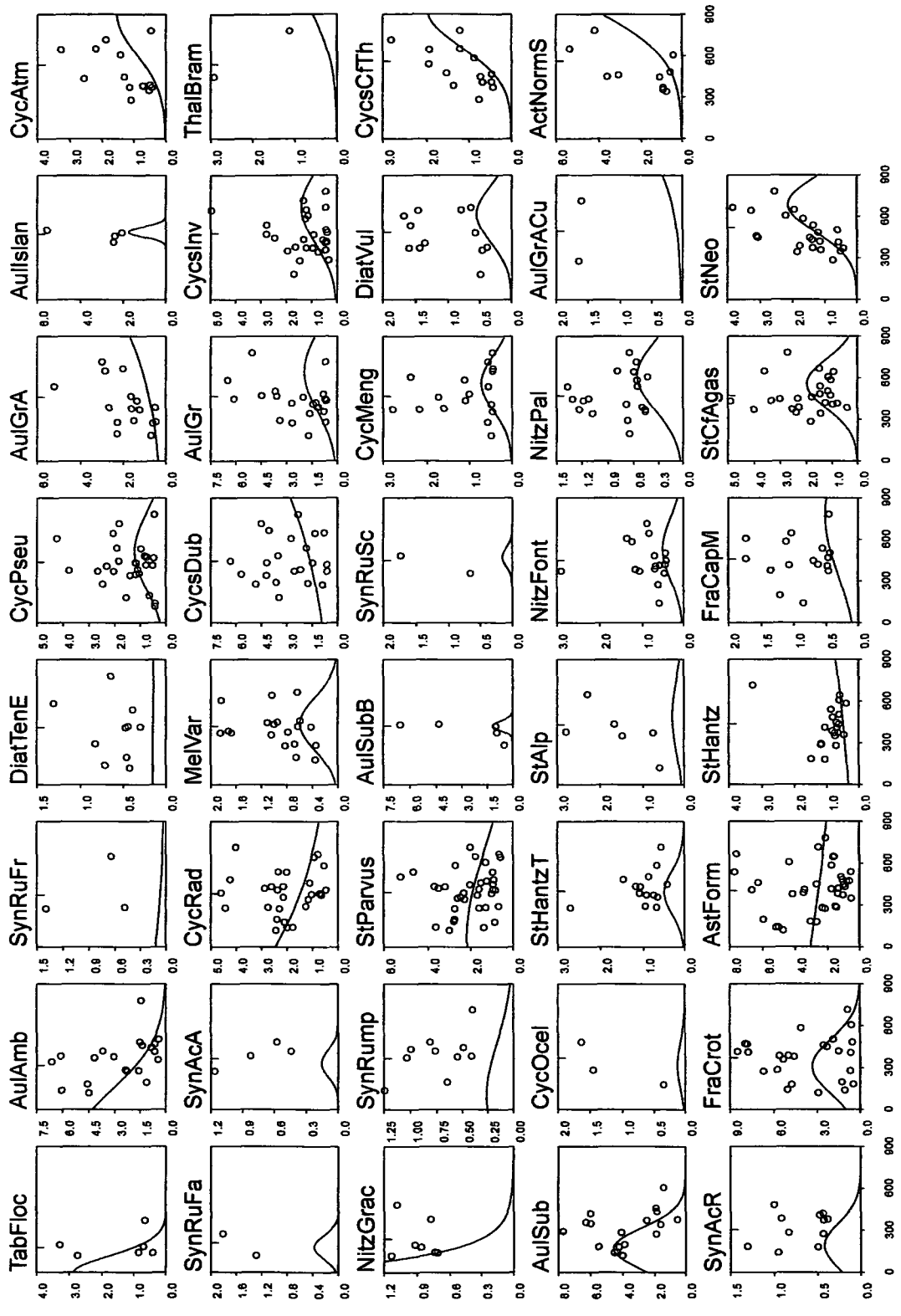


Figure 7.11b Plots illustrating square-root transformed diatom species percentage relative abundance ($\sqrt{\ }$ %) against annual mean EC concentration (log_{10} μScm^{-1} EC) for the plankton-only dataset (40 sites and 39 species). Tick marks show the estimated species optima for each species and the curves are the modelled response under logistic regression (LOGIT) (predicted unimodal fit). Species are ordered according to EC optima.

Species distribution	Full dataset		Plankton-only dataset	
	number	%	number	%
Unimodal	44	**53**	19	**49**
Truncated (lower end)	6	**7**	4	**10**
Truncated (upper end)	12	**15**	4	**10**
No clear trend	21	**25**	12	**31**

Table 7.14 Classification of diatom species distributions in relation to EC for both the full and plankton-only datasets.

Most diatom taxa (approximately 50%) show a unimodal distribution to EC. This may indicate that a higher proportion of species in the EC inference model have optima that are better-defined than those calculated under the TP and Chla inference models, in addition to having species with a narrower tolerance range. Perhaps this signifies that in general, species show less tolerance to changes in EC concentrations than to changes in TP. The narrower tolerances and well-defined EC optima of many diatom species helps to explain why the DI-EC model performs better than those developed to infer TP and Chla.

7.6.3 Comparative performance of the DI-EC models created for UK lowland reservoirs with those published in the literature

There can be only a limited discussion of the comparative performance statistics of models created in this study with those published in the literature. This is partly because many models relating diatom species to conductivity gradients (particularly the older models), measure salinity per se, and conductivity is expressed in different units to those used in this study. Many diatom-salinity models are constructed with the aim of using salinity as a proxy for the inference of climate change. In this study, the key aim was to maximise the trophic gradient. It was not originally envisaged that nutrient and conductivity gradients would be so intimately linked and that in the process of maximising the trophic gradient, a relatively long conductivity gradient would become an important feature of the dataset.

Examination of the data presented in Table 7.15 implies that the DI-EC models created in this study using both the full and plankton-only datasets compare favourably in terms of performance statistics (RMSEPs) with the models developed by Gasse *et al.* (1995) and Reed (1998). This is encouraging, since the EC gradient covered by this study is very short (119–781 μScm^{-1}) in comparison to that covered by the Spanish salt lake dataset (150–338000 μScm^{-1}) of Reed (1998) and the African lakes dataset (40-99060 μScm^{-1}) of Gasse *et al.* (1995). The reservoirs in this study span a relatively wide conductivity gradient in terms of the range of concentrations seen in freshwaters. However the range is far shorter than that from freshwater to ephemeral saline lakes covered by the models of Gasse *et al.*

(1995) and Reed (1998). The DI-EC models created in this study probably suffer less from a heterogeneous range of conductivities. Instead it would be expected that many species would exhibit truncated distributions at the high end of the conductivity gradient. However, results presented in Table 7.14 indicate that relatively few taxa appear to have underestimated EC optima because few show truncated distributions at the upper end of the EC gradient. This is probably because only 'freshwater' reservoirs have been sampled and many of the so-called 'freshwater' diatom taxa may be living at or near the upper limit of their salinity tolerance, but salinity levels are not yet at levels sufficiently high for 'brackish' water species to take over.

Compared with the models constructed for UK lowland reservoirs, the model of Ryves *et al.* (2002) performs better in terms of its r^2 value, but performs slightly worse in terms of its predictive ability. This may be because Ryves *et al.* (2002) sample a longer EC gradient but there are few examples of either high or low conductivity sites to enable robust prediction of EC at the extremes of the EC gradient. Alternatively as reported by Reed (1998), the diverse range of lake types sampled in her study added to the heterogeneity of her dataset and hence the relative influence of other environmental variables on diatom distributions may have been greater than in the UK lowland reservoirs calibration set.

Author	Area	No. of samples	Range (μScm^{-1})	Method	r^2 app. (boot)[1] (jack)[2]	app. RMSE (log μScm^{-1}) ($RMSE_{boot}$)[1] ($RMSEP_{jack}$)[2]	Trans-formation
Burgess (current study)	England (lowland reservoirs)	42	119-781 mean 424 median 417	WA, inverse deshrinking	0.84 (0.72)[2]	0.08 (0.10)[2]	log *x* EC √ species
		40 plankton	119-781 mean 414 median 413	WA, inverse deshrinking	0.79 (0.65)[2]	0.09 (0.11)[2]	log *x* EC √ species
Ryves *et al.* (2002)	West Greenland (lakes)	38	24-4072 mean 721 median 197	WAPLS (2)	0.96 (0.88)[2]	0.12 (0.22)[2]	log *x* EC
Reed (1998)	Spain (salt lakes)	55	150-338000	WA, inverse deshrinking	0.91 (0.57)[2]	0.18 (0.41)[2]	log *x* EC
Gasse *et al.* (1995)	Africa (lakes)	274	40-99060	WA, inverse deshrinking	0.87 (0.81)[2]	0.32 (0.39)[2]	-

Table 7.15 Comparison of the performance of DI-EC inference models created in this study with those published in the literature

7.7 General discussion of DI-TP, DI-Chla & DI-EC model performance

Although diatom species' optima are derived from models that appear to be statistically robust, it is clear that this approach over-simplifies the real-world environment. However, since this is the aim of environmental modelling it is not a failing of the approach but

rather, it should be recognised that the environment is inextricably complex and species rarely respond to perturbations of single environmental variable. Fritz *et al.* (1993b, p.19) comment that, "although modern calibration data sets provide information on the ecological tolerances of various diatom species, they may not include all the significant limnological variables. Therefore, despite strong correlations between diatom distributions and the measured trophic variables, it may not be possible to identify the real factors driving changes in species composition." Another point worth considering is that many environmental variables are highly correlated (Table 4.6) further increasing the difficulty of unravelling a single variable driving limnological change. However variance partitioning results shown in Figures 5.8 and 5.14, for both the full and plankton-only datasets respectively, indicate that there is little overlap between the explanatory power of ionic concentration / nutrient availability and water clarity / biological productivity in the UK lowland reservoir dataset. This is further exemplified by the presence of two distinct axes of variation (Figures 5.7 and 5.12). Therefore whilst inference models may not be able to delineate the influence of intercorrelated environmental variables, they can be used as a tool to identify broad changes in reservoir systems along these two axes of variation. It is unlikely however that the models will be capable of picking up smaller scale perturbations, where there are less well-defined shifts in species composition (Fritz *et al.*, 1993b). This may be particularly true in reservoir sequences dominated by diatom species with broad tolerances to the environmental variable under reconstruction. The ecological tolerances of key species are critical since their stratigraphy in core sequences is a major determinant of reconstructed values. It is perhaps unwise to hold too much confidence in the reconstructed values if species have both broad tolerances and poorly defined optima.

In addition, poorly defined species' optima affect the ability of inference models to accurately describe the distribution of diatom taxa along the ecological gradients of interest. Species distributions may be truncated and hence a taxon's optimum poorly predicted. Graphical representations of species distributions shown in Figures 7.5, 7.8 and 7.11 help to improve our understanding of the underlying species distribution patterns, thus enabling a more objective evaluation of model performance. This may be of particular relevance when applying the models to core sequences dominated by species for which optima are poorly defined.

The optima of taxa may not be adequately described by a relatively small, regional dataset such as that used in the current study (~40 sites). Inference models constructed from combined regional calibration datasets e.g. Bennion *et al.* (1996), can help to extend

environmental gradients and hence reduce the likelihood of truncated species distributions. However, as stressed by Bradshaw & Anderson (2001), care should be exercised in the application of datasets ill designed for the site or region under study, particularly where TP ranges and hence reconstructed values are consistently higher / lower. A further drawback of this approach is that taxa are harmonised in the process of dataset merging and in so doing some ecological information is invariably lost. This may ultimately affect the predictive ability of models. Therefore the best option may be to restrict calibration sets to specific lake typologies and to sample as many sites of a specific type as possible. This approach will obviously have logistical constraints, but may be preferable to combining datasets that do not 'fit'. In this study, the dataset size is partially constrained by available sites, but model performance appears to be enhanced by the limitation of sites to the reservoir typology and the inclusion of only sites meeting other prescriptive criteria (see Chapter 3). In addition, the calibration set created in the current study is composed of one main habitat – the plankton. This avoids problems associated with habitat heterogeneity that are inherent in calibration sets composed of sites where surface sediment assemblages comprise a diverse mixture of both planktonic and periphytic taxa (Sayer, 2001).

Thus reconstructed values can only be as good as the calibration dataset allows. This will be discussed further in the following chapter when the inference models are applied to core data. Further discussion of this important issue will also be pursued in Chapter 9.

7.9 Summary points

- UK lowland reservoirs are suitable sites for the development of robust inference models for inferring TP, Chla and EC. In this case EC inference models produce the lowest prediction errors and TP and Chla models perform comparably.
- Models developed for DI-TP, DI-Chla and DI-EC using WA inverse deshrinking show the strongest statistical performance for both the full and plankton-only datasets. The WAPLS(2) model developed for DI-TP for the full dataset shows the lowest RMSEP and lowest mean and maximum bias statistics, however the improvement in RMSEP over the simple WA inverse deshrinking model is only 1-2 % (i.e. <5% improvement). The WA classical deshrinking models perform less well overall, although they produce less bias in the residuals.
- The models developed in the current study are comparable in terms of statistical performance to those published in the literature.

- Plankton-only models perform almost as well as those using the full dataset. This is probably because the UK lowland reservoirs calibration set is composed of one main habitat - the plankton.
- The development of inference models for UK lowland reservoirs extends the range of lake typologies for which inference models have been created. The opportunity is presented for the incorporation of these sites into larger, combined datasets, extending the geographical and lake typology coverage. However caution should be exercised in combining such datasets.
- Models created in this chapter can be used to assess changes in reservoir water quality related to nutrient enrichment (TP), biological productivity (Chla) and catchment disturbance (EC). This information is of potential benefit in the assessment of past perturbations and the development of future reservoir management strategies.

CHAPTER EIGHT

Application of inference models

8.1 Introduction

In the previous chapter diatom-based inference models were developed from a calibration set of UK lowland reservoirs for the inference of TP, EC and Chla. In this chapter these inference models are applied to dated sediment core diatom stratigraphies from two selected UK lowland reservoirs, with the aim of reconstructing historic water quality. The timing and extent of observed diatom species shifts and diatom-inferred water quality reconstruction trajectories are interpreted through examination of historic records relating to land-use change and reservoir management practices, and in the light of published results from similar studies.

8.2 Potential of reservoirs for sediment coring and inference model application

This section discusses factors influencing the selection of two contrasting reservoir sites at which to reconstruct TP, Chla and EC. It does not seek to rule out the application of the inference models at individual sites; rather the aim is to ensure that the two sites selected provide intact diatom sedimentary records that span a sufficient time period for the rigorous evaluation of the reconstruction capabilities of the models created in Chapter 7. Several factors including reservoir age, diatom preservation and previous reservoir management practices are considered (summarised in Table 8.1).

8.2.1 Reservoir age

In this study, it is considered most appropriate to select reservoirs with sedimentary records spanning as long a time period as possible. This should increase the probability of the fossil diatom remains recording past perturbations and recoveries from for example, enhanced nutrient loadings due to population expansion, intensification of agriculture and discrete pollution incidents. UK lowland reservoirs are generally rather young (<100 years BP) and only 15 sites in this study are over 50 years old. To obtain the longest possible chronological sequence, further consideration of coring suitability was limited to the 15 oldest sites.

Reservoir	Date completed	and age (years)	Depth of diatom preservation	Potential long-coring site?	Reasons for potential or exclusion in this study
Ardleigh	1979	21	-	No	Age
Blackbrook	1906	94	Throughout reservoir's history – no dissolution	Yes	Well-preserved diatom record with evidence of diatom species shifts following impounding reservoir
Blagdon	1901	99	5-6cm preservation good 24-26cm breakage & dissolution	No	Dissolution with increasing depth – only central areas intact as depth increases
Blithfield	1953	47		No	Age
Cheddar	1938	62		No	Unusual diatom assemblage
Chelmarsh	1966	34		No	Age and sediment removed in 1990s after pollution incident
Chew Valley	1953	47	6-8cm preservation OK 14-16cm preservation OK	Potential, although rather young	Age and evidence of dissolution with depth (although recovered cores show contradictory trends)
Clatworthy	1959	41	-	No	Age
Costessey	1940	60	-	No	Size & short residence time
Cropston	1870	130	-	No	Dredged in 1970s
Draycote	1969	31	< 8cm	No	Age and dissolution >8cm
Durleigh	1939	61	-	No	Dredged at shallow western end
Eyebrook	1940	60	5–6cm preservation OK 18–20cm quite dissolved	No	Dissolution evidence with increasing depth
Foxcote	1956	44	-	No	Age
Grafham	1966	34	< 8cm	No	Dissolution evidence and reservoir very young
Hollowell	1938	62			Dissolution >8cm
Leigh	1893	107	10-11cm preservation OK	No	Dredged in 1980s
Luxhay	1905	95	-	No	Reservoir has been emptied and some sediment has been dredged
Nanpantan	1870	130			Unusual diatom taxa & dredged?
Ogston	1960	40	-	No	Age
Pitsford	1956	44	-	No	Age
Porth	1960	40	-	No	Age
Ravensthorpe	1890	110	< 8cm only	No	Dissolution >8cm
Rutland	1977	23	-	No	Age
Stanford	1928	72	< 7cm only	No	Dissolution >7cm
Staunton Harold	1966	34	-	No	Age
Stithians	1967	33	-	No	Age
Sutton Bingham	1956	44	-	No	Age
Swithland	1894	106	Throughout reservoir's history – no dissolution	Yes	Well-preserved diatom record Similar to Blackbrook
Thornton	1854	146	-	No	Reservoir emptied, scraped and cleaned in 1950-51
Tittesworth	1963	37	-	No	Age
Trenchford	1907	93	4-6cm preservation OK 24-26cm preservation OK	Potential	No evidence of dissolution but unusual diatom assemblage
Trimpley	1971	29	-	No	Age
Upper Tamar	1976	24	-	No	Age
Wimbleball	1979	21	-	No	Age
Wistlandpound	1953	47	-	No	Age
Ardingly	1979	21	-	No	Age
Arlington	1971	29	-	No	Age
Bewl	1975	25	-	No	Age
Bough Beech	1968	32	-	No	Age
Darwell	1950	50	-	No	Age
Powdermill	1932	68	6-7cm preservation poor 12-13cm no diatoms	No	Preservation poor. Sediment sulphurous, with iron oxides
Weir Wood	1953	47	-	No	Age
Daventry	1804	196	Preservation throughout 45cm short core	Yes, post-1900s	Diatom preservation good, but reservoir dredged in early 1900s

Table 8.1 Suitability of UK lowland reservoir sedimentary records for evaluation of diatom-based palaeolimnological inference models. Sites with long, well-preserved sedimentary records are shaded.

8.2.2 Dredging, reservoir management and reservoir-specific factors

Historic records detailing reservoir management practices and engineering activities were investigated to establish the likely integrity of the sediment stratigraphy in the 15 sites demonstrating potential (in terms of age) for palaeolimnological investigation.

The oldest reservoirs have often been dredged at some time in their history, perhaps unsurprising since sediment accumulation results in reduced water storage capacity. This is an undesirable situation for water supply reservoirs, because under-utilisation of potential storage capacity leads to decreasing reservoir efficiency.

Since many UK lowland reservoirs are relatively young, dredging activities have often occurred too recently to allow the subsequent accumulation of sediments representing an adequate temporal sequence. This is the case at Cropston, Leigh and Thornton reservoirs, which are all over 100 years old, but have all undergone de-silting in the latter half of the 20th century. Other sites excluded due to management issues were Costessey and Nanpantan reservoirs. These sites are both very small and have short residence times. Although there is no direct evidence that these sites have been dredged in the past, it is not unreasonable to assume that dredging or sediment disturbance has occurred due to their small volumes.

8.2.3 No analogues

In addition, Nanpantan's surface sediment diatom assemblage has a high percentage relative abundance of *Cyclotella comensis* (29%) (Table 5.14), a taxon absent from the surface sediments of all other reservoirs in the calibration set. Cheddar and Trenchford present a similar problem to Nanpantan in that their surface sediment diatom assemblages comprise a number of periphytic and (tycho)planktonic taxa absent from the calibration set or of rare occurrence (e.g. *Aulacoseira alpigena*, *Synedra tenera* and *Gomphonema minutum*). As a result, the reconstruction capabilities of the inference models at these sites would probably be limited. Only 10% of Cheddar's and 39% of Trenchford's (Table 5.14) surface sediment diatom assemblages consist of (tycho)planktonic diatom taxa, which obviously presents a problem in applying the plankton-only models and is of further concern in that the full models comprise predominantly (tycho)planktonic taxa.

8.2.4 Diatom preservation and dissolution

Diatom preservation in the sediments of the remaining reservoirs was examined to assess their potential for the application of diatom-based inference models. Dissolution of diatoms was frequently observed below ~8 cm sediment depth in many reservoirs (Table 8.1). Thus

a limited number of reservoirs showed potential for the application of inference models. Possible mechanisms for dissolution and poor diatom preservation are discussed in Chapter 2.

Unfortunately, problems associated with dissolution were not confined to the youngest reservoirs. For example, Blagdon was constructed in 1901 and both dissolution and breakage were evident with increasing depth. Ravensthorpe and Hollowell were constructed in 1890 and 1938 respectively but again, diatom preservation was poor below ~8 cm. Powdermill dates back to the 1930s, but diatom preservation was poor even towards the top of the core and the sediments were both sulphurous and stained orange with iron oxides. Other reservoirs that were relatively old but showed poor preservation of diatoms included Stanford (1928) and Eyebrook (1940).

8.2.5 Blackbrook and Swithland reservoirs

Blackbrook Reservoir was the initial site selected for inference model application and evaluation. Previous diatom analyses by Sayer (unpublished) and examination of selected levels in short cores retrieved in the current study, highlighted the integrity of this reservoir's diatom record. In addition, the diatom profile revealed species shifts indicative of progressive eutrophication. This was considered valuable for the application of a TP inference model, potentially providing the opportunity to demonstrate relationships between TP and diatom community structure. Opportunities were originally thought to exist for the validation of the inference model using historical water chemistry data collected by Severn Trent Water (STW). However, this option was later abandoned due to difficulties of data harmonisation and the absence of TP measurements prior to the late 1990s.

In common with its geographical neighbour Blackbrook, Swithland Reservoir appeared to have a full, well-preserved diatom record. However the species assemblages and shifts observed in Swithland's sediments were similar to those seen in Blackbrook. It was decided therefore that examination of sediment cores from both Blackbrook and Swithland would not enable the comprehensive evaluation of inference model capabilities under conditions of differing diatom species assemblages. The selection of an additional site with both contrasting characteristics and diatom populations was considered more appropriate.

8.2.6 Daventry reservoir

Daventry Reservoir was not originally selected either as a sampling site or as a potential site for inference model application. However during the course of this study, Daventry District

Council sought a palaeolimnological study of Daventry's sediments, the main aim of which was to investigate the effect on the reservoir's ecosystem of grit trap installation and sewage-works decommissioning. This was to be achieved through examination of sediment geochemistry and biological indicators, including the diatom data presented in this study, in dated sediment cores. Preliminary examination of Daventry's sedimentary sequence indicated that diatoms were present throughout and that there was evidence of temporal changes in diatom community structure, possibly correlated with documented historical events at the site. It was not considered important that Daventry's sediments had been dredged in the early 1900s because interest lay in the effects of activities carried out in the 20th century, and sufficient sediment had since accumulated to provide a comprehensive record. Daventry's diatom stratigraphy showed contrasting characteristics to those seen in Blackbrook, providing opportunities to test the inference capabilities of the transfer functions across a broader range of species assemblages. As with Blackbrook, inference model validation was deemed inappropriate due to difficulties with historical data acquisition and quality.

8.3 Blackbrook reservoir

8.3.1 Background information

Blackbrook reservoir in Leicestershire (OS grid ref: SK458175), lies at an altitude of 111 m.a.O.D., receiving an annual rainfall of approximately 750mm (Read, 1990). The Charnwood Forest area in the Borough of Charnwood has been important for Leicestershire's water supply since the late nineteenth century (Read, 1990). Blackbrook is one of four surface-water supply reservoirs lying within Charnwood's boundary. Only about 20% of Leicestershire's water supply comes from within the county, the remainder coming principally from the Rivers Dove and Derwent in Derbyshire (Read, 1990). Blackbrook is owned and managed for water supply by Severn Trent Water (STW), although at the present time 10 Ml day^{-1} is the maximum volume of water available for extraction. STW does not currently consider Blackbrook of major importance for water supply.

Site history

Unrelated to water supply, the original Blackbrook reservoir / pool was constructed between 1791 and 1794 to feed the Charnwood Forest Canal. In 1799 however, the earth dam was washed away by storm water. Although the dam was repaired, it was eventually dismantled and the reservoir abandoned in 1804, when the canal scheme proved a failure. The canal was subsequently in-filled and re-developed as a railway (Newton, 1984).

The inauguration of the Charnwood Forest water-supply reservoirs at Cropston, Nanpantan, Swithland and Blackbrook was a direct result of the demands of the rapidly expanding industrial City of Leicester, the population of which grew from 68,000 to 211,000 in the forty years between 1861-1901 (Crocker, 1981). The first of the reservoirs to be constructed was Cropston, opening in 1870. The Nanpantan Reservoir (Wood Brook Scheme) was subsequently implemented in 1871. This reservoir and treatment works were constructed at an elevation that would permit augmentation from the Black Brook if the need arose (Newton, 1984). Greater capacity was soon required to supply sufficient water to the rapidly expanding population in the Borough of Loughborough. This resulted in the passing of plans in 1897 for the creation of Blackbrook Reservoir. The site of the original reservoir was re-surveyed and dam construction commenced in 1899. It was completed in 1906 with the flooding of the valley by the then Loughborough Corporation Waterworks (Newton, 1984).

The reservoir lies in an area strewn with geological faults (Read, 1990), and on 11th February 1957 an earthquake, with its epicentre at Diseworth (four miles north of the Blackbrook dam), struck the region. It was recorded as VII on the Modified Mercalli Scale, which is amongst the strongest shocks recorded in Britain. The reservoir dam received a 'severe shock' (Newton, 1984), and the water level was drawn-down as a precautionary measure. Although cracks appeared in the masonry, the dam was, after inspection, certified to be safe. On May 30th 1984 another earthquake was experienced. This was less severe, recording 2.7 on the Richter Scale, with its epicentre in north Leicestershire; no further damage was inflicted to the dam (Newton, 1984).

Figure 8.1 Blackbrook reservoir July 1999. Bubbles generated by the destratification equipment can be seen running diagonally across the deepest part of the reservoir (from the boat on the left, to the edge of the photo on the right).

Blackbrook was equipped with destratification apparatus in ~1990 (John Smith, STW, pers. comm.) This consists of a bubble curtain extending diagonally across the deepest part of the reservoir in proximity to the dam wall (Figure 8.1).

Underlying geology and soils

Leicestershire is one of the most important mineral producing counties in the UK. The Charnwood area provides significant quantities of igneous rock and slate for both the building trade and highway construction (Read, 1990). The geology underlying Blackbrook Reservoir and its catchment consists of ancient Precambrian Charnian rock of the Blackbrook series in the Charnwood Forest area, alongside younger more easily eroded red mudstones of the Triassic Keuper Marl in the valleys within and surrounding the Forest. The Charnian Rocks are the most ancient (approx. 700-800 million years BP) of the Precambrian rocks of Charnwood and have been much altered over time. They are of volcanic origin, formed from layers of ash (tuff), mud and occasionally lava, sometimes embedded with breccia (Read, 1990).

The upland soil overlying the Charnian Rocks is of the Iveshead series, a brown, loamy, well-drained acidic soil poor in nutrients, particularly potash. This soil frequently supports rough moorland, but in many areas has been improved by the addition of lime and fertilizers to enable crops of cereal and grass to be grown (Crocker, 1981). The soil overlying the Keuper Marl is less acidic, richer in potash (derived from its higher clay fraction), but similarly deficient in available phosphate (Crocker, 1981).

Catchment land use

Blackbrook is an impounding reservoir, receiving water from its sole inflow stream, the Black Brook and its catchment of approximately 12.2km^2. Figure 8.2 illustrates the extent and land-use composition of Blackbrook's catchment. Land use in the catchment comprises predominantly mixed farming (~80%) with small areas of mixed woodland (Crocker, 1981). There are a number of silage pits within the catchment associated with intensive pastoral agricultural practices (Ian Evans, English Nature, pers. comm.). Figure 8.2 shows that the M1 motorway is routed across the south east of Blackbrook's catchment and a number of B-roads also pass through the catchment. Blackbrook's catchment is entirely rural and houses in the catchment are not connected to a mains sewerage system. Domestic sewage is contained in septic tanks (Ian Evans, English Nature, pers. comm.). It is clear that there are

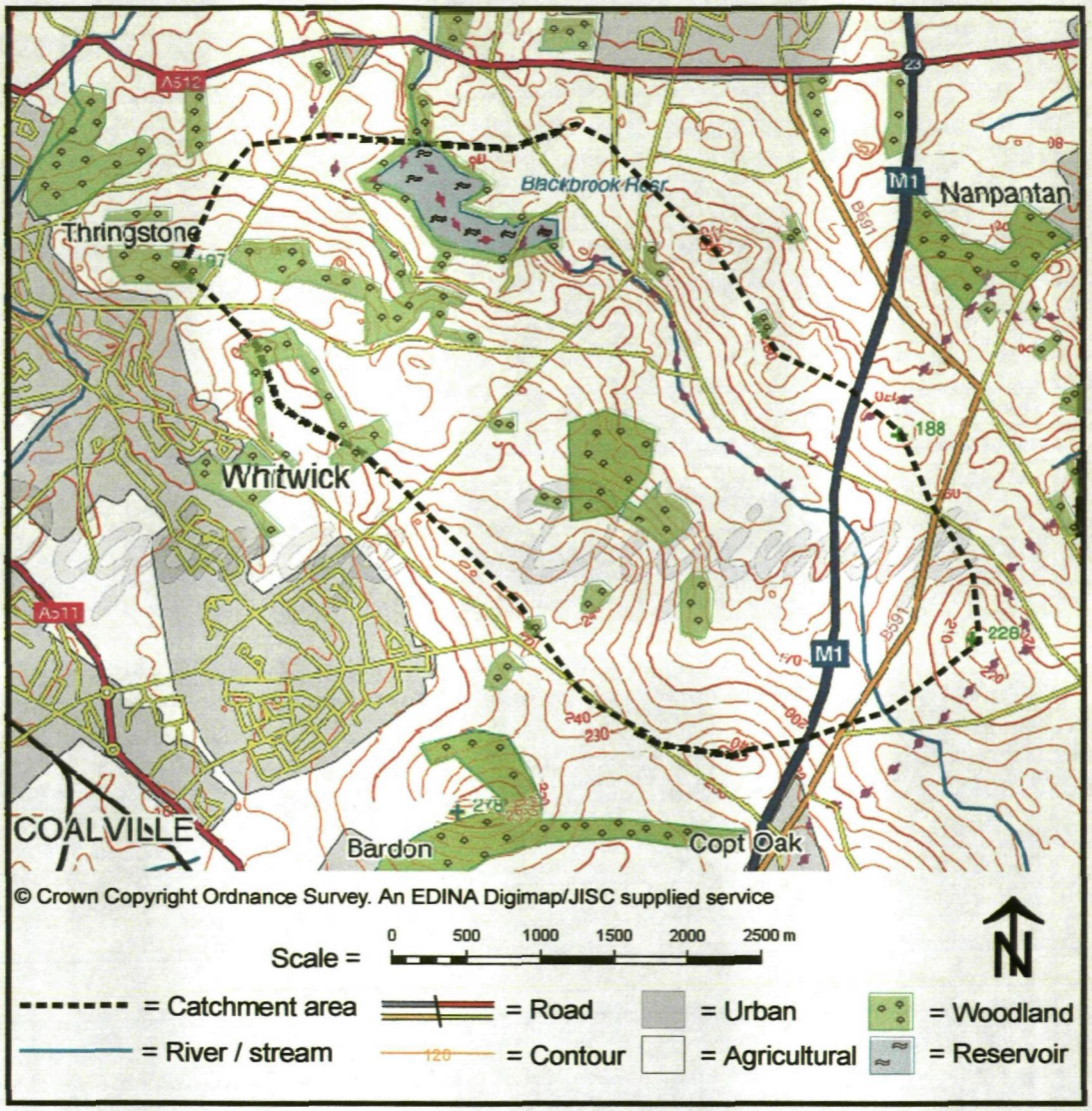


Figure 8.2 Catchment area and land use map for Blackbrook reservoir

a number of possible diffuse pollution sources that could impact on Blackbrook's water quality.

Conservation interest

In 1985 the reservoir was notified (under Section 28 of the Wildlife and Countryside Act 1981) as a SSSI in recognition of both its biological and geological importance. At the time of notification, the reservoir was described as being "mesotrophic" and supporting a "most unusual marginal plant community unique to the English Midlands and reminiscent of that found in a few sites in northern England" (English Nature website). The mesotrophic water was said to be derived from the admix of acid base-poor Precambrian rocks of the Blackbrook series and the more fertile base-rich Triassic and glacial deposits. At notification, the marginal plant and aquatic plant community at Blackbrook comprised a "great abundance" of the uncommon thread rush, *Juncus filiformis* growing at its most

southerly location in England. Further species supplementing the "unusual mix" included small water-pepper *Polygonum minus*, lesser marshwort *Apium inundatum*, floating club-rush *Eleogiton fluitans*, shore-weed *Littorella uniflora* and pond water crowfoot *Ranunculus peltatus*. Species reflecting a more southerly or base-rich influence were trifid bur-marigold *Bidens tripartita* and lesser pond sedge *Carex acutiformis* (English Nature website).

When Blackbrook was notified as an SSSI, its secluded valley was said to provide a wintering ground for locally important flocks of wintering wildfowl (Crocker, 1981) and supported breeding great crested grebe and little grebe as well as native crayfish *Austropotambius pallipes* isolated from populations of the alien American crayfish (English Nature website).

The site is not open to the public, although members of a private fishing club fish from both the bank and boats for stocked brown trout (*Salmo trutta* L.) and coarse fish. Although STW owns Blackbrook reservoir, the Leicestershire and Rutland Wildlife Trust jointly manage the site for conservation.

Carvalho & Moss (1995) reported that Blackbrook's SRP concentration was 120 μgl^{-1}, classifying the site as 'hypertrophic'; possible pollution sources were unknown. Although conservation interest was not reported to have changed since SSSI notification, further investigation was recommended.

During the summer and autumn sampling periods in both 1999 and 2000, Blackbrook was dominated by blooms of the blue-green alga *Microcystis* spp. Poor water clarity resulted in a paucity of submerged macrophyte growth. Although only a limited area of the reservoir was sampled for aquatic macrophytes, in July 1999 *Polygonum amphibium*, rooted in the sediment and with floating leaves at the water surface, was the dominant, though sparse, macrophyte growing to a depth of approximately 2m. There was also evidence of *Callitriche* spp. and the filamentous alga *Cladophora* spp. In the late summer of 2000, *Cladophora* spp was dominant. Blackbrook's conservation interest as a 'mesotrophic' site may therefore be threatened. When English Nature last assessed Blackbrook's status in December 2001, the reservoir's condition was classified as "unfavourable declining". Water quality was deemed to have become too poor to support the feature of interest (i.e. mesotrophy) that determined Blackbrook reservoir's original SSSI notification. High phosphorus concentrations from diffuse pollution sources were considered to be the cause of deteriorating water quality (English Nature website).

8.3.2 Blackbrook's sedimentary record (core BBK00C)

This section presents the results of Blackbrook's sedimentary record in terms of coring location, lithology and lithostratigraphy.

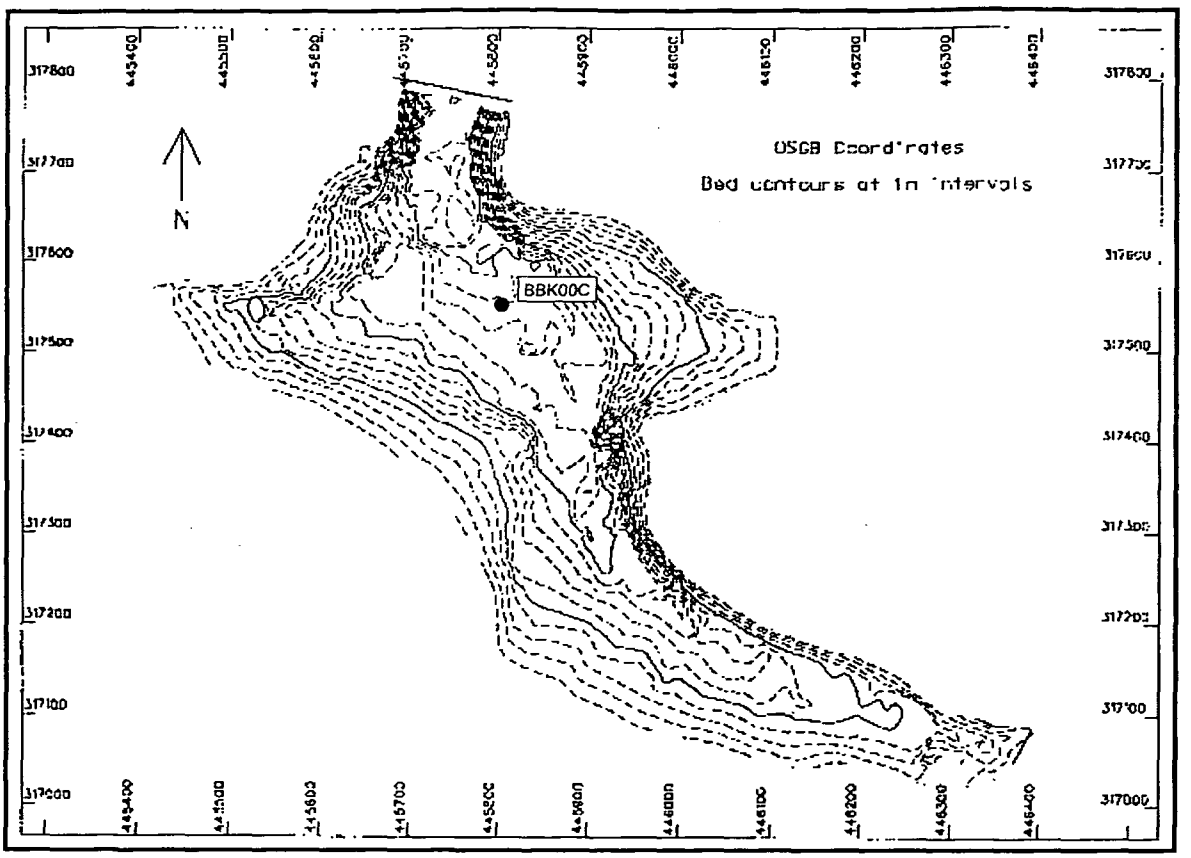


Figure 8.3 Bathymetric map illustrating the location of core BBK00C. The dam wall is located at the northern end of the reservoir and the main inflow channel (the Black Brook) enters from the southeast (Source D. Twigg, Loughborough University Civil Engineering Department).

Coring location for BBK00C

BBK00C was extracted on 28/06/2000 at grid reference SK4579717547 and from a water depth of 13.7 m (Figure 8.3). The coring site was selected on account of its moderately deep depth and as a site of potential sediment focussing (Sly, 1978; Battarbee, 1986; Davis, 1996). As can be seen from the wide distance between adjacent contours, the coring site was relatively flat, purposefully avoiding steeply shelving banks and areas immediately adjacent to these, which could be influenced by sediment reworking particularly during periods of reservoir drawdown. The coring site also avoided the deepest area of the reservoir because of the possibilities of sediment disturbance arising from destratification and draw-off activities. Inflow channels were avoided for similar reasons.

Sediment lithology

Table 8.2 presents the sediment lithology description of core BBK00C. The 0-12 cm section comprises dark brown lake mud, the top 1 cm of which is slightly paler and less consolidated than that below. From 12–43 cm the sediment is darker and appears to be more anaerobic. Below 43 cm, the sediment becomes increasingly gritty containing a dense network of plant roots and appears to be the underlying mineral soil.

Depth (cm)	Description
0-1	Pale brown fluid lake mud
1-12	Dark brown lake mud
12-43	Black organic-rich lake mud
43-47	Gritty black organic-rich lake mud
47-70	Mineral soil (containing roots)

Table 8.2 Sediment lithology of core BBK00C

Core sections shaded in Table 8.2 contain little or no diatom remains and were therefore not used for diatom analysis. This left a diatom sequence of 43 cm, thought to represent Blackbrook Reservoir's entire 20th century history, with the earliest sediments dating back to its inauguration as a water-supply reservoir in 1906.

Sediment lithostratigraphy

Figure 8.4 illustrates the percentage dry weight (%DW), percentage LOI (%LOI) and percentage $CaCO_3$ (%$CaCO_3$) profiles for core BBK00C.

From the core base (48 cm) to 36.5 cm, %DW decreases rapidly from 58% to 27%. %DW then shows a slight but steady overall decrease (28 to 20%) from 36.5-4.75 cm, increasing again from 4.75 cm, to a peak of 25% at 2.75 cm, but dropping to 22% from 2.75-0.0 cm.

%LOI results indicate that the organic matter content of Blackbrook's sediments has increased over its most recent history, showing the general trend of lower %LOI towards the core base and higher %LOI towards the core top. From the core base (48 cm) to 42.5 cm, %LOI increases from below 10 to 14%, then between 42.5-10.5 cm %LOI remains fairly stable and generally below 15%. Above 10.5 cm, %LOI increases, fluctuating between 15-17%.

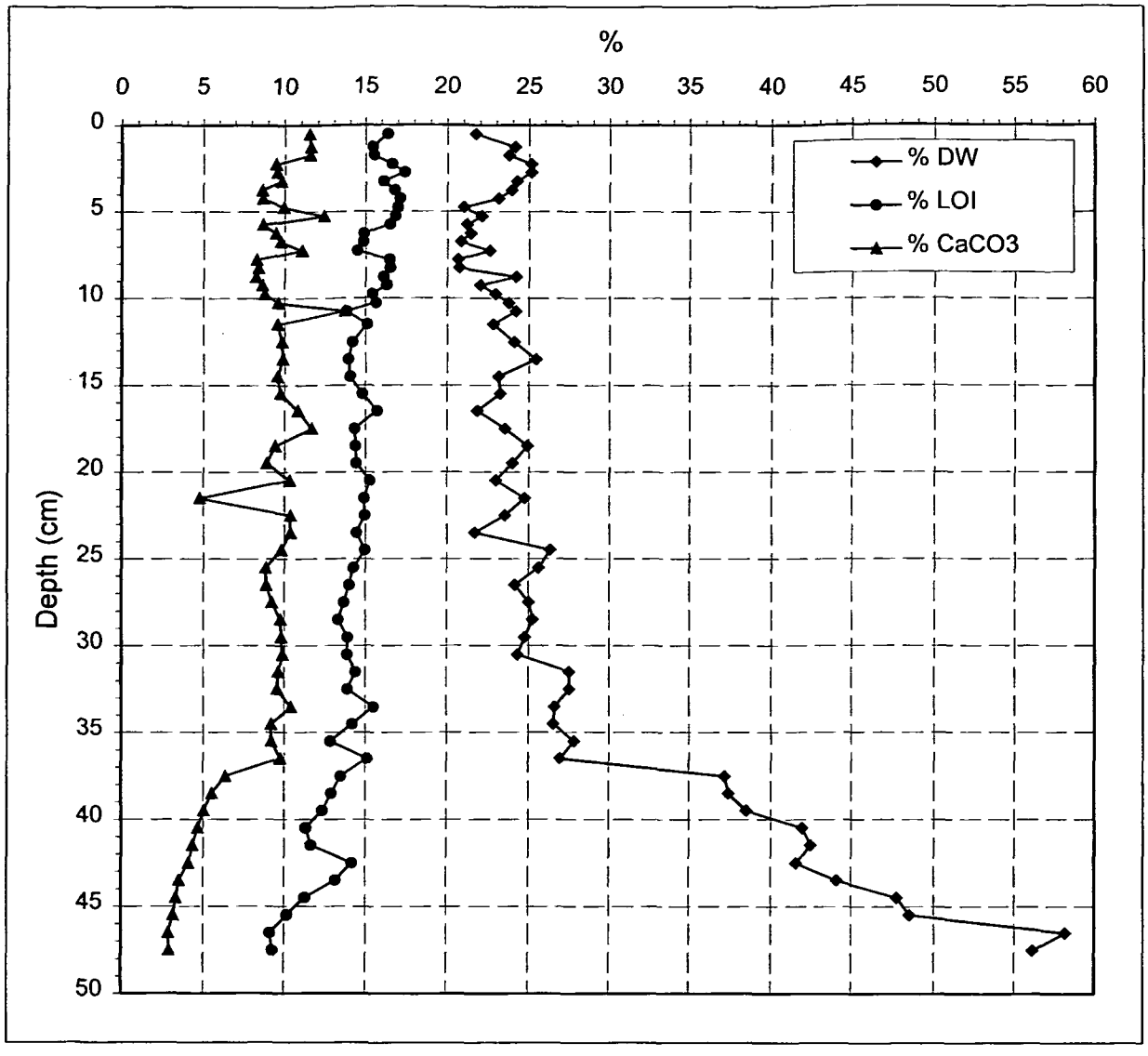


Figure 8.4 **Sediment lithostratigraphy for core BBK00C, illustrating percentage dry weight (%DW), percentage organic matter (%LOI) and percentage calcium carbonate (%$CaCO_3$).**

%$CaCO_3$ is very low (~4%) at the core base, probably reflecting the depleted $CaCO_3$ content of the mineral soil in Blackbrook's catchment. From the core base (48 cm) to 36.5 cm %$CaCO_3$ increases to 10%. Above 36.5 cm %$CaCO_3$ remains relatively stable at ~10% to 1.75 cm but between 1.75 cm to the core top %$CaCO_3$ increases slightly to 11.5%.

The distinct change towards more stable %DW, %LOI, and %$CaCO_3$ conditions at ~37 cm in core BBK00C may indicate the development and subsequent stabilisation of Blackbrook's aquatic ecosystem following its inauguration as a water-supply reservoir in 1906. This progression may be comparable to the process of ontogeny seen in the development of natural lakes (Deevey, 1984).

A provisional outline chronology for BBK00C

Unfortunately, accurate radiometric dating results are not available for core BBK00C. However, sediment cores were taken from Blackbrook reservoir and analysed for diatoms by Barker (unpublished) and Sayer (unpublished) in 1987 and 1991 respectively. The diatom stratigraphies from both these cores have upper sediment assemblages that are dominated by *Aulacoseira islandica* (40-60% relative abundance) and show no evidence of *Thalassiosira pseudonana*. Comparing these earlier stratigraphic records with that in the current study, it has been assumed that the year 1990 is approximately attributable to a core depth of ~4-5 cm (see section 8.3.3 for a discussion of BBK00C's diatom stratigraphy). Based on the assumption that Blackbrook reservoir has maintained a constant (linear) sedimentation rate of ~0.4-0.5 cm per year, a provisional outline chronology has been devised. Since this is only a provisional chronology, it is only used to enable a fuller discussion in section 8.3.5 of the timing of Blackbrook reservoir's trophic state changes in relation to available historic records. Despite the overall assumption of a constant sedimentation rate, deviations from a linear trend may have occurred over time. Sedimentation rate may have been higher in Blackbrook's initial phase of development, perhaps due to a greater input of clastic material from catchment sources (Figure 8.4). Sedimentation rate may have also increased with eutrophication since there is no marked decrease in %DW in Blackbrook's more recent sediments. Furthermore, there may have been a hiatus in sedimentation at a depth of ~38 cm, where %DW decreases markedly and $\%CaCO_3$ and %LOI increase in tandem (Figure 8.4). Deviations such as these may increase the errors associated with the assumption of a linear sedimentation rate throughout Blackbrook's history. However, the assumed sedimentation rate of ~0.4-0.5 cm per year derives a date for the core base of between 1894 and 1915, the mid-point of which is consistent with construction of the reservoir in the year 1906.

8.3.3. Blackbrook's diatom stratigraphy

A total of 25 levels from BBK00C were analysed for diatoms. Table 8.3. displays diatom cell concentrations calculated using the microsphere method, diatom biovolumes, the total number of diatoms counted in each level, the total number of diatom taxa recorded in each sample and the associated floristic diversities (See Chapter 3 for methods and Appendix 4 for details of biovolumes used).

The number of diatom valves counted in each sample ranges from 372–759 (mean = 528 ±87), the average number of diatom taxa per sample is 32 ±5 (range 21-39) and the floristic diversity (number of taxa divided by total valve count) ranges from 0.04-0.08 (mean = 0.06

Sample depth (cm)	Total number of taxa	Total valve count	Floristic diversity	Diatom concentration Microsphere method (cells g^{-1} DW $x10^6$)	Diatom biovolume (μm^3 g^{-1} DW $x10^9$)
0.75	29	566	0.05	-	-
1.25	30	564	0.05	87.06	142.41
1.75	38	634	0.06	48.06	98.88
2.25	39	507	0.08	42.11	63.64
2.75	39	537	0.07	44.99	84.81
3.25	34	478	0.07	43.19	87.43
3.75	27	515	0.05	53.86	97.67
4.25	30	552	0.05	55.23	96.43
4.75	36	510	0.07	60.17	125.38
5.75	34	487	0.07	59.95	104.01
6.75	36	601	0.06	98.33	160.92
7.75	34	406	0.08	72.92	95.37
8.75	34	536	0.06	100.50	105.57
9.75	32	759	0.04	110.57	88.34
12.50	29	660	0.04	103.68	53.40
15.50	21	553	0.04	124.23	47.95
18.50	27	588	0.05	117.28	45.11
21.50	31	468	0.07	123.23	61.56
24.50	30	474	0.06	89.43	55.17
27.50	38	528	0.07	59.74	64.07
30.50	25	406	0.06	63.79	27.12
33.50	34	590	0.06	53.54	65.21
36.50	36	505	0.07	42.23	30.80
39.50	25	405	0.06	18.95	10.76
42.50	24	372	0.06	8.21	3.67
Mean	32	528	0.06	70.05	75.65
Median	32	528	0.06	60.06	75.01
Min	21	372	0.04	8.21	3.67
Max	39	759	0.08	124.23	160.92
SD	5	87	0.01	32.36	39.06

Table 8.3 Diatom cell concentrations, counts and diversity statistics for BBK00C.

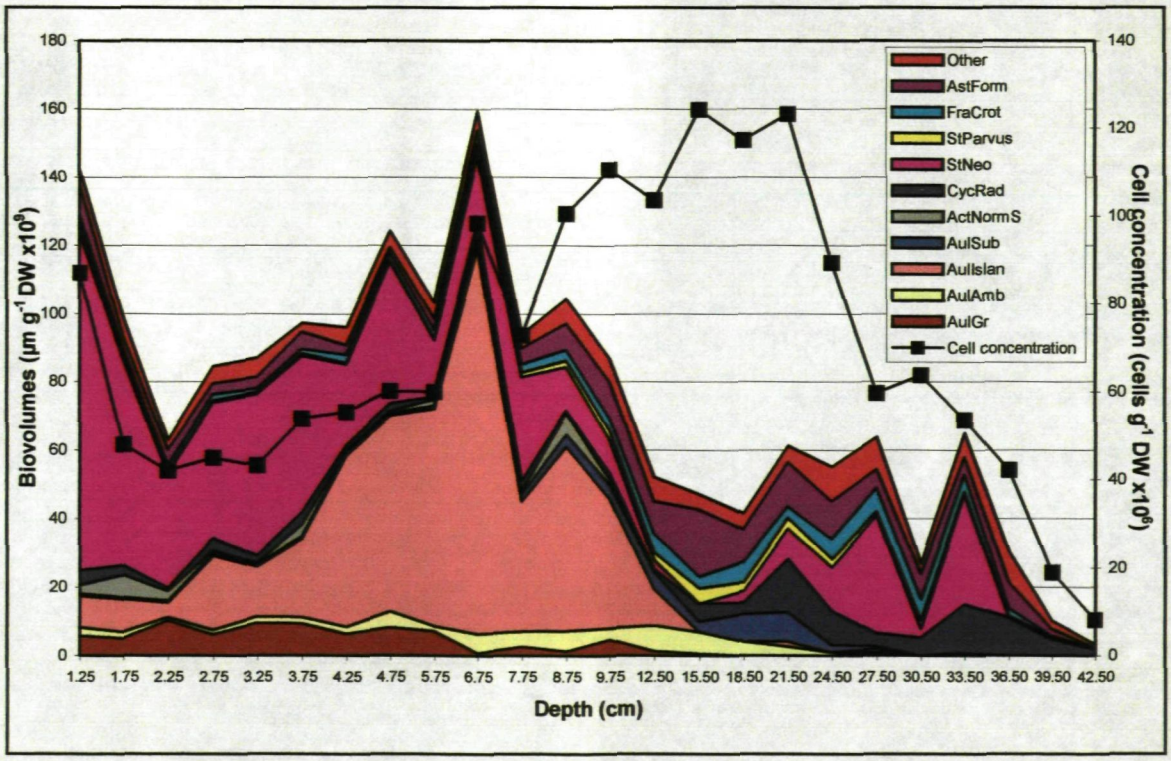


Figure 8.5 Diatom cell concentrations and biovolumes for core BBK00C. (Note that depth scale is not regularly spaced and is related to sample number).

±0.01). Floristic diversity is at its lowest between 8.75-18.5 cm, coinciding with the period of maximal cell concentrations, indicating that diatom concentrations are high but dominated by few taxa.

Figure 8.5 shows that diatom cell concentrations and biovolumes follow similar trends between 0 and 9.0 cm, with lower overall cell concentrations but larger biovolume taxa dominating. Taxa contributing most to overall biovolumes in this section of the core are the large centric taxa, *S. neoastraea* and *A. islandica*, with cell biovolumes of 16837 and 2714 μm^3 respectively. Between ~9.0 and 32.5 cm, cell concentrations increase to their highest levels and then remain high (100-125 cells g^{-1} DW $x10^6$), whereas biovolumes decrease rapidly and then remain relatively low (45-65 μm^3 g^{-1} DW $x10^9$). This discrepancy is interpreted as a period in the fossil record comprising large populations of *S. parvus*, *A. subarctica*, *F. crotonensis*, *A. formosa* and *A. ambigua*. These taxa are small in terms of cell size and thus biovolume (cell biovolumes of 108, 202, 358, 496 and 618 μm^3 respectively). Below 32.5 cm, both diatom cell concentrations and biovolumes decrease markedly to their lowest levels (8.21 cells g^{-1} DW $x10^6$ and 3.67 μm^3 g^{-1} DW $x10^9$ respectively) at the base of the core. *C. radiosa* (cell biovolume = 2105 μm^3) contributes an increasing proportion of overall diatom biovolume in this section of the core, despite *S. parvus* (cell biovolume = 108 μm^3) occurring at the highest percentage relative abundance.

In core BBK00C, only 17 diatom taxa occur at ≥3% relative abundance in one or more samples. Of these taxa 15 can be classified as (tycho)planktonic and 2 (*Fragilaria vaucheriae* and *Achnanthes minutissima*) are periphytic, indicative of the dominance of planktonic diatom taxa throughout Blackbrook's history. This is unsurprising, since Blackbrook has always been a relatively deep reservoir with, for the most part, steeply shelving banks and a limited littoral zone. The reservoir's mean secchi depth is ~2 m (Table 4.3) and its mean depth is ~7 m (Table 3.1), indicating that the photic zone does not extend to the bottom sediments across much of the reservoir.

Figure 8.6 illustrates the summary diatom data for core BBK00C. Only the 17 taxa occuring at ≥3% relative abundance in one or more samples are presented. Shown alongside are overall percentages of planktonic/periphytic taxa and the diatom cell concentrations and biovolumes. Also shown are diatom-inferred TP, Chla and EC reconstructions using the full models, which are discussed in section 8.3.4.

The diatom stratigraphy can be divided into 5 local diatom assemblage zones (B-1 to B-7). Zone boundaries were determined by a stratigraphically constrained incremental sum-of-squares cluster analysis (CONISS; Grimm, 1987) using a square-root transformation and chord-distance dissimilarity measure for all diatom taxa in the 25 sample levels. In stratigraphic order, the zone boundaries are 38.0 cm, 23.0 cm, 14.0 cm, 7.25 cm, 4.0 cm and 1.0 cm.

Zone B-1, 42.5 cm - 38.0 cm:

This zone is characterised by the dominance of the small centric diatom *S. parvus* (30-50%). Also present in moderate abundance in this zone are both *Cyclotella radiosa* (~10%) and *Diatoma tenuis* var. *elongatum* (~10%) and *Asterionella formosa* increases in abundance from ~6-25%. *Fragilaria crotonensis* appears at trace values towards the top of this zone. The proportion of periphytic diatom taxa is ~15-20% and consists mainly of *A. minutissima*. %LOI is at its lowest levels in this zone. $\%CaCO_3$ steadily increases throughout this zone from ~4.1-6.4% (Figure 8.4). This may indicate that Blackbrook's ecosystem is developing and becoming more productive, supporting the evidence for increases seen in diatom cell concentrations and biovolumes throughout B-1. This is in line with observations that increasing phytoplankton bioproductivity results in higher sedimentary calcium carbonate precipitation (Rippey *et al.*, 1997; Lotter, 1989).

Although diatom cell concentrations and biovolumes are low in B-1 (8-19 $x10^6$ cells g^{-1} DW and 3-11 $x10^9$ μm^3 g^{-1} DW respectively), the diatom frustules show no evidence of dissolution. This is of particular note in respect of *D. tenuis* var. *elongatum*, which is weakly silicified and therefore would readily show signs of dissolution (cf. Ryves *et al.*, 2002) if this phenomenon were a problem in core BBK00C. This suggests that the changes in diatom populations seen in this zone and throughout the core, are 'real' and unbiased by the processes of dissolution and differential preservation.

Zone B-2, 38.0 cm - 23.0 cm:

This zone sees the co-dominance of *F. crotonensis*, *A. formosa* and *S. parvus*. *C. radiosa* and *D. tenuis* var. *elongatum* decrease in percentage relative abundance throughout zone B-2, whereas *Aulacoseira subarctica* and *Aulacoseira ambigua* appear for the first time at low values. Diatom cell concentrations rise steadily throughout this zone, from ~30 to ~100 $x10^6$ cells g^{-1} DW.

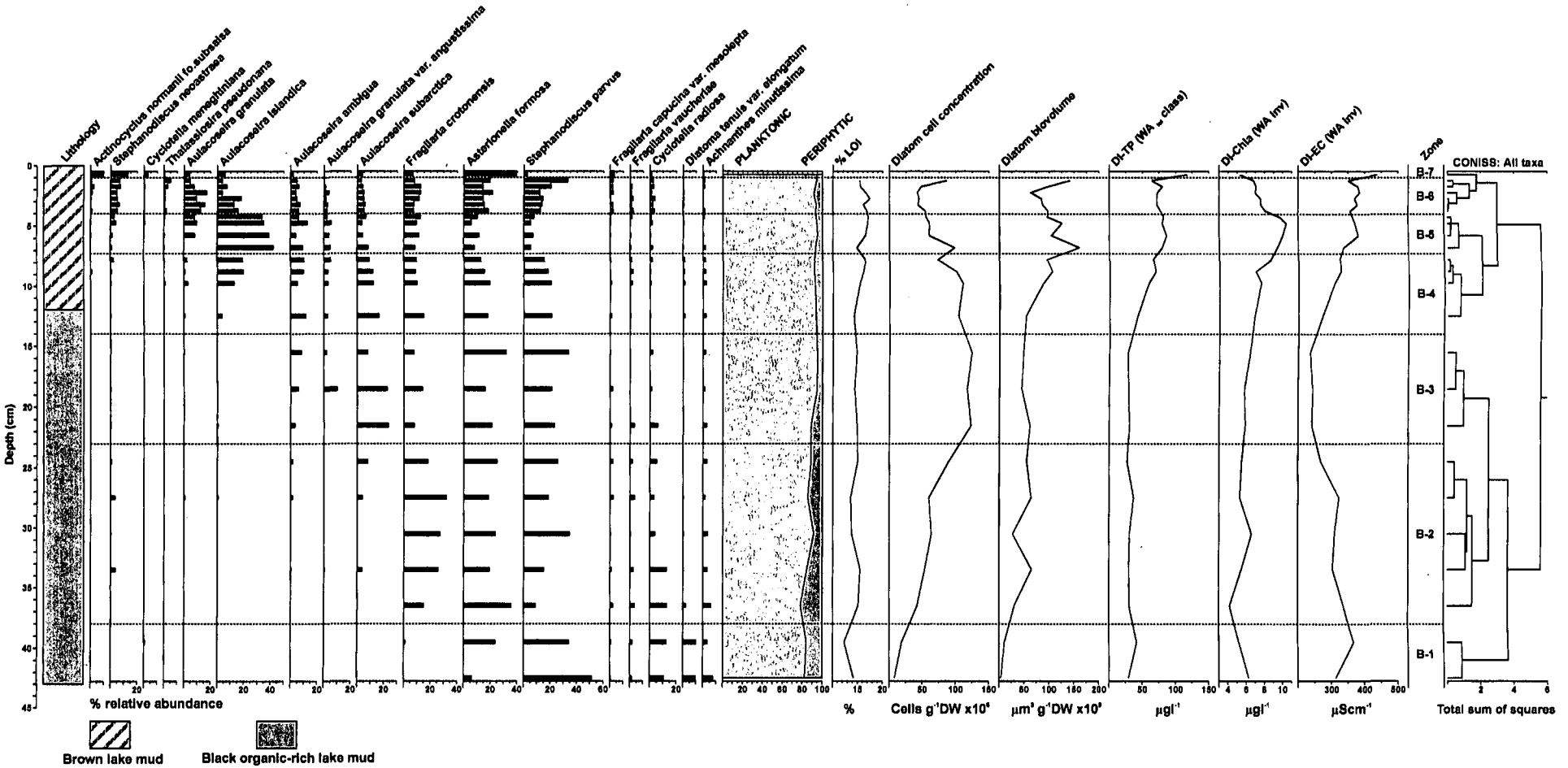


Figure 8.6 Stratigraphic profiles of the dominant species, diatom habitats, %LOI, diatom population statistics and diatom-inferred reconstructions (full model) in BBK00C (only taxa occurring with ≥3% abundance in one or more samples are shown).

Zone B-3, 23.0 cm – 14.0 cm:

This zone sees an increase in the percentage relative abundance of *A. subarctica* to ~20%. *A. ambigua* occurs at low, but steadily increasing values. *A. formosa* and *S. parvus* continue to co-dominate, although *A. subarctica* replaces *F. crotonensis* as an additional co-dominant. *F. crotonensis* continues to occur but at a lower percentage relative abundance than in earlier zones. Diatom cell concentrations are at their highest (~120 $x10^6$ cells g^{-1} DW) and most stable in zone B-3, although diatom biovolumes remain relatively low and constant at ~45-60 $x10^9$ μm^3 g^{-1} DW. %LOI is stable in this zone.

Zone B-4, 14.0 cm – 7.25 cm:

Aulacoseira islandica increases in importance throughout this zone. *S. parvus*, *A. formosa*, *A. subarctica* and *A. ambigua* continue to occur, but at lower values. *C. radiosa* occurs in its lowest percentage relative abundance in this zone. *Thalassiosira pseudonana* and *Actinocyclus normanii* fo. *subsalsa* appear for the first time at 9.75 cm and 8.75 cm respectively and *Aulacoseira granulata* consistently occurs at low percentage relative abundance. Diatom cell concentrations decrease in zone B-4 (100-~80 $x10^6$ cells g^{-1} DW) and biovolumes increase, reflecting the increasing percentage relative abundance of the large-celled *A. islandica*. % LOI also steadily increases in zone B-4 (~14-16.5%).

Zone B-5, 7.25 cm – 4.0 cm:

A. islandica is the dominant diatom taxon in zone B-5, occurring at ~30-40% relative abundance. *S. neoastraea* and *A. granulata* increase in percentage values throughout this zone. *Cyclotella meneghiniana* occurs at very low percentage values and *T. pseudonana* continues to occur at similarly low abundances. *A. ambigua*, *Aulacoseira granulata* var. *angustissima*, *A. subarctica*, *F. crotonensis*, *A. formosa* and *S. parvus* occur at overall lower percentage values than in zone B-4. Diatom concentrations and biovolumes increase at the start of this zone (to ~100 $x10^6$ cells g^{-1} DW and ~160 $x10^9$ μm^3 g^{-1} DW respectively), coinciding with the marked increase in *A. islandica*. However cell concentrations and biovolumes then decrease towards the top of this zone (to ~50 $x10^6$ cells g^{-1} DW and ~100 $x10^9$ μm^3 g^{-1} DW respectively). %LOI continues to increase to ~17%, following an initial drop at the start of this zone, coinciding with the marked increases in diatom cell concentrations, biovolumes and proportion of *A. islandica*.

Zone B-6, 4.0 cm – 1.0 cm:

The most striking change in this section of BBK00C is the decline in percentage relative abundance of *A. islandica*. *A. formosa* and *S. parvus* increase in percentage values throughout this zone. *A. granulata* occurs at its highest values in B-6 (~10-15%), although its abundance decreases with decreasing depth. Although *T. pseudonana* occurs at low percentage values, its proportional representation increases throughout B-6 to ~5%. *A. granulata* var. *angustissima* disappears at the top of this zone. Both diatom concentrations and biovolumes decrease slowly at the start of this zone, before increasing markedly at the top of B-6. %LOI fluctuates, although there is a slight decreasing trend.

Zone B-7, 1.0 cm – 0.0 cm:

Zone B-7 consists of only one sample, but its diatom species composition is distinctly different from that seen in the previous zone. *S. parvus*, frequently a dominant taxon throughout BBK00C, decreases significantly in percentage relative abundance in this zone. Instead, *A. formosa* dominates zone B-7 (~40%); this is a taxon that typically blooms in the vernal period (e.g. Figure 6.7). The large centric diatoms *S. neoastraea* and *A. normanii* fo. *subsalsa* occur at ~13% and 10% relative abundance respectively, their highest at any point in the core sequence. These diatom taxa are typically found in reservoir plankton samples during the summer and autumn period (Chapter 6). Therefore Zone B-7 is interpreted as a seasonal sampling artefact. This sample has not undergone taphonomic processes such as dissolution and breakage and has thus not yet become a true fossil sample. Instead it reflects a recently deposited bloom (cf. Bennion, 1994; Bennion *et al.*, 1996; Sayer 2001).

8.3.4 Reconstructing Blackbrook: Diatom-inferred total phosphorus (DI-TP), chlorophyll-*a* (DI-Chla) and conductivity (DI-EC) reconstructions

This section presents for Blackbrook reservoir, the results of DI-TP, DI-Chla and DI-EC reconstructions based on the most appropriate model (WAPLS or WA/WA_{tol} using either classical or inverse deshrinking methods) for each variable (TP, Chla and EC) and for each dataset (full and plankton-only).

Selection of reconstruction models

Table 8.4 displays details of the models selected for environmental reconstructions at Blackbrook along with the reasoning behind these choices. The models selected for reconstruction of TP were not the same as those selected as 'the best' in terms of performance statistics during the development of the inference models in Chapter 7 (Table

7.3). When applying models to core sequences, there are further considerations aside from performance statistics. Examination of tolerances for the most abundant and frequently occurring diatom taxa in BBK00C reveals that in relation to TP the majority have tolerances higher than mean values (e.g. for the full model *A. ambigua* = 20% higher and *A. formosa* = 14% higher). Therefore it is appropriate to apply a model using tolerance downweighting since this method takes species tolerances into account by downweighting each species by its variance for the environmental variable in question (TP in this case). Reconstructions based on simple WA and WA_{tol} produce similar overall reconstruction trajectories and the models show similar performance statistics. Since WA_{tol} models account for broad species tolerances and since for the full dataset, WA_{tol} classical best predicts Blackbrook's current mean annual epilimnetic TP concentration (118 μgl^{-1} -Table 4.3), this model is considered the most appropriate for TP reconstruction of core BBK00C. The plankton-only model that best predicts Blackbrook's current TP concentration, accounts for broad species tolerances and displays the best predictive statistics is that using WA_{tol} inverse deshrinking.

Variable	Choice of models for the full and plankton-only diatom inferred reconstructions	
	Full	**Plankton-only**
TP	**WA_{tol} classical** a) Majority of most abundant and frequently occurring taxa show higher than average tolerance for TP (5-20% higher than mean value) b) RMSEP as low as WA inverse and WAPLS(2) models (0.23), although mean and max bias slightly higher c) Surface sediment DI-TP concentration closest to current epilimetic TP	**WA_{tol} inverse** a) Majority of abundant and frequently occurring taxa have higher than average tolerance for TP (6-33% higher than mean value) b) Lowest RMSEP of all models, although mean and max bias not as low as for simple WA models
Chla	**WA inverse** a) Lowest RMSEP of all models and low mean and max bias b) Few of the most abundant / most frequently occurring taxa have tolerances higher than the mean value	**WA inverse** *(see full model for reasoning)*
EC	**WA inverse** a) Lowest RMSEP of all models and low mean and max bias b) Surface sediment DI-EC concentration closest to current epilimetic TP c) Most abundant and frequently occurring taxa show a range of tolerances both above and below mean values	**WA inverse** *(see full model for reasoning)*

Table 8.4 Inference models selected for environmental reconstructions at Blackbrook reservoir and the reasoning behind these choices

The models chosen for DI-Chla reconstruction, using both the full and plankton-only datasets, are identical to those selected as 'the best' in terms of model performance in Chapter 7 (Table 7.7). Few of the most dominant species in BBK00C demonstrated

tolerances above mean values and all display mean values ≤12% for the full dataset and ≤8% for the plankton-only dataset. For the surface sediment assemblage, the simple WA inverse deshrinking model infers Chla values in close proximity to Blackbrook's current mean annual Chla concentration of 5.5 μgl^{-1} (Table 4.3).

In common with DI-Chla models, those models selected for EC reconstruction under both the full and plankton-only datasets are the same as those selected as 'the best' in terms of model performance in Chapter 7 (Table 7.12). Although over half of the dominant diatom taxa in BBK00C show higher than average tolerances, the models using tolerance downweighting considerably over-predict current EC levels. Current mean annual EC measured for Blackbrook reservoir is 406 μScm^{-1}. The simple WA models reconstruct surface sediment values of 420-425 μScm^{-1}, as opposed to 540-570 μScm^{-1} reconstructed under the WA_{tol} models. This discrepancy may occur because the process of downweighting the dominant species enables those species with narrower tolerances, and possibly higher EC optima, to exert a greater influence on the reconstructions.

Diatom-inferred total phosphorus reconstruction (DI-TP)

Figure 8.7a shows the DI-TP reconstruction for BBK00C according to the WA_{tol} classical deshrinking model and based on the full dataset. The standard errors of prediction (SEPs) estimated by bootstrapping indicate that the maximum errors in the model could be as much as double the reconstructed values. These SEPs are comparable with those reported for similar DI-TP model reconstructions, e.g. Rippey *et al.* (1997), Bennion *et al.* (1995) and Tibby (2004).

The DI-TP reconstruction shows three distinct phases, starting with a stable and relatively low DI-TP (25-40 μgl^{-1}) from 42.5 cm to 15.5 cm, with prediction errors showing maxima of 50-70 μgl^{-1} and minima of 15-20 μgl^{-1}. This suggests that during this phase the reservoir was, in respect of DI-TP at the upper end of the 'mesotrophic' classification of freshwaters according to OECD (1982) criteria (see Figure 4.4).

Subsequent to this period of relative stability, the reconstruction indicates a second phase, showing a sharp increase in DI-TP between 15.5-5.75 cm in which DI-TP increases from 28-87 μgl^{-1}. According to OECD classifications, the water becomes 'eutrophic' at the beginning of this phase, between 15.5-12.5 cm, followed by a further doubling of DI-TP concentrations between 12.5 and 5.75 cm, to take DI-TP into the upper range of TP concentrations encompassed by the 'eutrophic' OECD (1982) category.

Following this period of increasing DI-TP concentrations, values remain high, subsequently becoming more stable towards the core top (4.75–1.75 cm), fluctuating over a narrow range of DI-TP concentrations (71-83 μgl^{-1}). The core surface appears to give somewhat erratic reconstructions, with DI-TP shifting from 80 μgl^{-1} at 1.75 cm, down to 64 μgl^{-1} at 1.25 cm and than up to 118 μgl^{-1} at 0.75 cm. This inconsistency in reconstructed values most likely reflects the influence of seasonal artefacts (Sayer, 2001). In this case it appears to be the high percentage relative abundance of *A. normanii* fo. *subsalsa* in the surface sediment sample which was shown in Chapter 6 to have produced substantial summer blooms in Blackbrook. This aside, reconstructed DI-TP concentrations at the core top indicate that the reservoir has now become established as a strongly eutrophic site according to OECD (1982) TP criteria.

Figure 8.7b shows that the full and plankton-only datasets predict very similar DI-TP concentrations and trends. The three clear phases described above are mirrored by the plankton-only dataset. The only notable difference between the model reconstructions is that the plankton-only dataset predicts slightly higher DI-TP concentrations throughout the core, particularly towards the sediment surface. This may occur because the full model contains periphytic taxa, which are generally found in greatest abundance and diversity in calibration set sites that exhibit lower TP concentrations.

Diatom-inferred chlorophyll-a reconstruction (DI-Chla)

Figure 8.7c illustrates the DI-Chla reconstruction for BBK00C according to the WA inverse deshrinking model and based on the full dataset. The SEPs estimated by bootstrapping are of similar magnitude to those seen for the DI-TP reconstruction and thus represent an acceptable range for the reconstructed concentrations.

As with the DI-TP trajectory, DI-Chla shows three distinct phases, starting with a relatively stable DI-Chla at the base of the Blackbrook core. Between 42.5 cm and 15.5 cm DI-Chla fluctuates between 4 and 6.5 μgl^{-1}, with SEPs showing maxima of 7-11 μgl^{-1} and minima of 2.5-4 μgl^{-1}. The DI-Chla reconstructions support the inference from the DI-TP results that during this period Blackbrook was a 'mesotrophic' freshwater according to the OEDC (1982) criteria (see Figure 4.4).

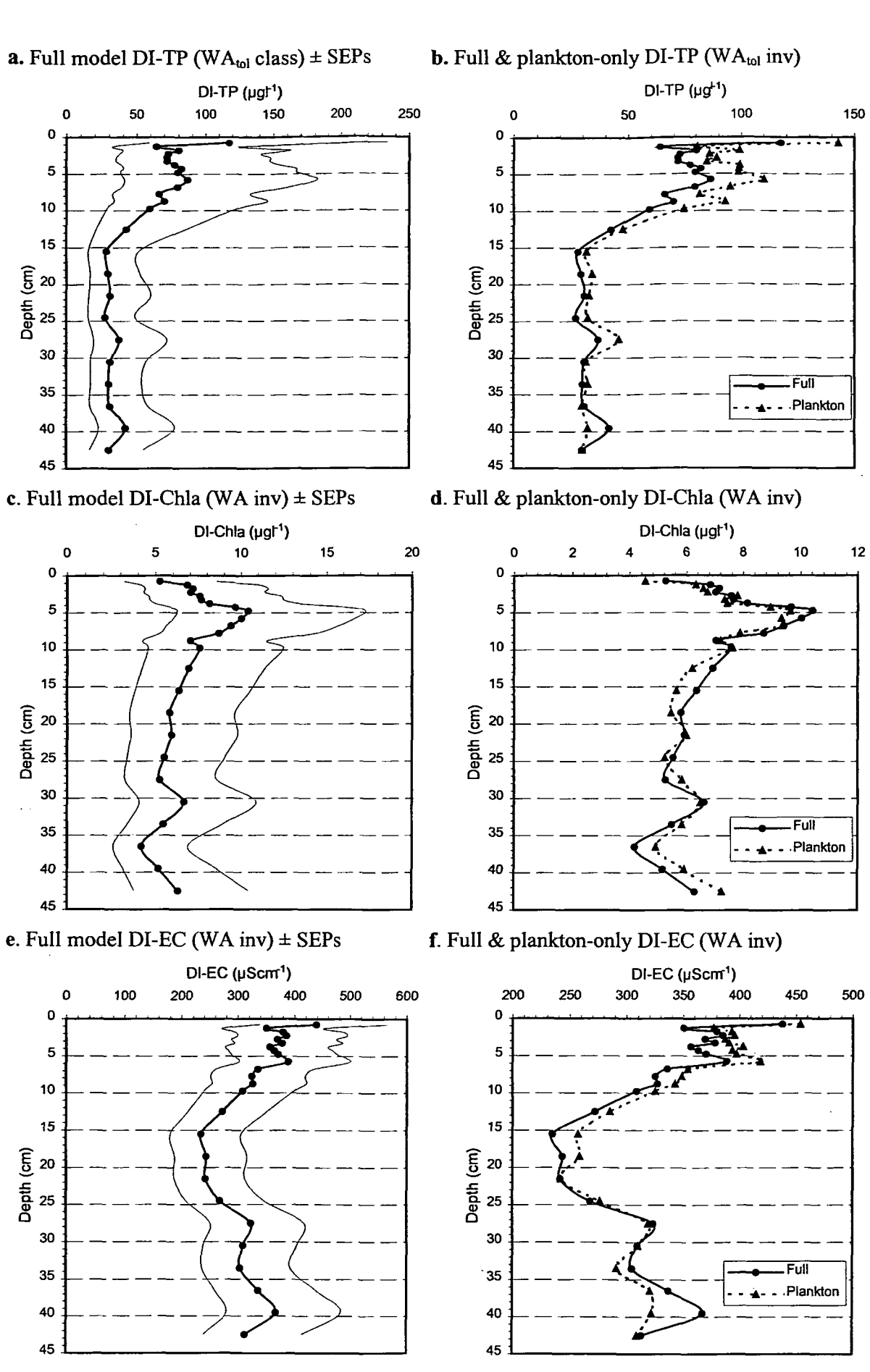


Figure 8.7 **Diatom-inferred TP, Chla and EC reconstructions of BBK00C. On the left are the full dataset model reconstructions (thick line) with standard errors of prediction (narrow lines). On the right are comparisons of the reconstructions from the full and plankton-only models.**

In common with the DI-TP reconstructions, DI-Chla begins to increase after this initial period of stability, rising from 6.4 μgl^{-1} at 15.5 cm to 10.4 μgl^{-1} at 4.75 cm. DI-Chla concentrations indicate that Blackbrook is increasing in trophic state, crossing the threshold at 7.75 cm from 'mesotrophic' to 'eutrophic' according to OECD (1982) Chla criteria.

Changes in DI-Chla towards the core top follow a slightly different trend to DI-TP. Instead of DI-Chla concentrations stabilising at a high level, implying a eutrophic status, DI-Chla decreases from 10.4 μgl^{-1} at 4.75 cm to 7.0 μgl^{-1} at 2.25 cm, where it stabilises until 1.25 cm. This reduces DI-Chla back to the upper region of the 'mesotrophic' category according to OECD (1982) Chla criteria. Unlike DI-TP, the penultimate sample (1.25 cm) does not show a significant deviation from the reconstruction trend, however the final sample (0.75 cm) does, decreasing a further 1.5 μgl^{-1}, to 5.3 μgl^{-1} at 0.75 cm.

The plankton-only model reconstructs a very similar DI-Chla trend to the full model (Figure 8.7d). There is no discernable difference in the reconstructed values or overall DI-Chla trend and the three phases outlined above can also be seen in the plankton-only reconstruction.

Diatom-inferred conductivity reconstruction (DI-EC)

Figure 8.7e shows the DI-EC reconstruction for BBK00C according to the WA inverse deshrinking model and based on the full dataset. The SEPs estimated by bootstrapping again show an acceptable range for the predicted values.

The DI-EC reconstruction can be divided into four distinct phases. In the section nearest the base of the core, from 42.5-27.5 cm, DI-EC fluctuates between 300-370 μScm^{-1}, with SEPs reaching maxima of 400-485 μScm^{-1} and minima of 235-280 μScm^{-1}. However after this initial period of fluctuation, DI-EC drops significantly from 323 μScm^{-1} at 27.5 cm to 235 μScm^{-1} at 15.5 cm.

From 15.5 cm, DI-EC follows a similar trend to DI-TP, increasing from 235 μScm^{-1} at 15.5 cm, to 389 μScm^{-1} at 5.75 cm. Following this period of increase and a peak in inferred values at 5.75 cm, DI-EC stabilises between 4.75-1.75 cm, showing values of between 350-385 μScm^{-1}. As with DI-TP, the top two samples show somewhat erratic reconstructions, decreasing to 351 μScm^{-1} for the 1.25 cm sample and increasing significantly to 438 μScm^{-1} in the 0.75 cm sample.

The plankton-only DI-EC model reconstruction (Figure 8.7f) shows similar values and follows a comparable trend to that shown by the full model, with the four phases outlined above clearly discernable. It does however show considerably more stable reconstructed DI-EC values, with markedly less fluctuation in the 42.5 cm-27.5 cm section.

8.3.5 Discussion of Blackbrook's history

Table 8.5 chronicles the historical and palaeolimnological record of Blackbrook reservoir. Unfortunately the actual timing of palaeolimnological events is not possible to assess at present due to the absence of accurate radiometric dating results. However the following discussion proposes possible explanations for the observed stratigraphic changes based on a provisional outline chronology that assumes a linear sedimentation rate of 0.4-0.5 cm per year (see section 8.3.2 for reasoning).

Blackbrook's sedimentary record indicates an initial period of post-construction aquatic ecosystem establishment, followed by a phase of relative stability and more recently an episode of nutrient enrichment. Zone B-1 (Figure 8.6) represents the transitional period in Blackbrook's history following completion of the reservoir in 1906 and the initial filling with water from its catchment. This period is seen as equivalent to the primary phase in the process of ontogeny in natural lakes (Chapter 2). It records a high relative abundance of *S. parvus* (~30-50%), along with a significant abundance of *D. tenuis* var. *elongatum* (~10%), the magnitude of which is not seen at any other time in Blackbrook's history. Both *S. parvus* and *D. tenuis* var. *elongatum* tend to bloom in the spring and are generally associated with relatively high nutrient concentrations (e.g. Stoermer, 1978, Anderson *et al.*, 1990). They are also taxa which are highly competitive under high concentrations of P (i.e. low Si:P ratios - Tilman *et al.*, 1982). Diatom cell concentrations and biovolumes are seen to increase steadily in zone B-1 (Figure 8.6) as populations of *S. parvus* and *D. tenuis* var. *elongatum* expand under initially high nutrient concentrations. Of further relevance to Blackbrook's history is the frequent occurrence of *D. tenuis* var. *elongatum* in studies charting the early stages of reservoir development. Atkinson (1988) presents data illustrating the dominance of *D. tenuis* var. *elongatum* in the spring diatom plankton (referred to as *Diatoma elongatum* (Lyngb.) in Atkinson, 1988) during the first year after the initial filling of Cow Green reservoir, northern England. The source of the initial species to become established in the reservoir was attributed to inocula from the inflow river and pools. Holz *et al.* (1997) reported on phytoplankton community response to reservoir ageing in Pawnee Reservoir, Nebraska, USA. The initial phase of development of this reservoir saw high TP and TN concentrations, accompanied by the presence of *Diatoma* spp., which

Decade	Historical or Known Events	Depths and provisional dates	Palaeolimnological Events
1790s	1791 -1794: Original reservoir / pool constructed as a canal feeder reservoir. 1799: Earth dam washed away by storm water and subsequently rebuilt.		
1800s	1804: Dam dismantled and reservoir abandoned.		
1890s – early 1900s	1897: Passing of plans for water supply reservoir. 1899 -1906: Construction of dam and filling of reservoir	Core base 43 cm (1904)	Reservoir sediment record commences
1905 – 1915		43–38 cm 1904–1916	Diatom zone B-1 Stabilisation period
1915 – 1950	1940s +: Agricultural intensification	38–23 cm 1916–1949	Diatom zone B-2 Mesotrophic phase (stable)
1950 – 1970	1957: Earthquake (large). Cracks appear in dam wall. Reservoir drawn down 1965: M1 motorway completed – increased road-salting likely	23–14 cm 1949–1969	Diatom zone B-3 Mesotrophic phase (stable)
1970 – 1985	1984: Earthquake (small) 1985: Blackbrook reservoir designated an SSSI on account of its 'mesotrophic' status	14–7 cm 1969–1984	Diatom zone B-4 Onset of eutrophication
1985 – 1990		7–4 cm 1984–1991	Diatom zone B-5 Eutrophic phase
1990s	Early 1990s: Destratification equipment installed (bubble-curtain) 1995: Carvalho & Moss (1995) report that Blackbrook's SRP concentration is 120 μgl^{-1}, and classify the site as 'hypertrophic' (possible pollution sources are unknown). Although conservation interest has not changed since notification, further investigation is recommended. 1999: Seasonal sampling programme for current study commences. Cyanophyte blooms present throughout summer and autumn	4–1 cm 1991–1998	Diatom zone B-6 Eutrophic phase
2000s	2000: Cyanophyte blooms present throughout summer and autumn 2001: SSSI condition classified as "unfavourable declining" by English Nature. Water quality deemed too low for mesotrophic classification and P from diffuse sources considered problematic	1–0 cm 1998–2000	Diatom zone B-7 Seasonal diatom artefact 2000: Sediment cores taken

Table 8.5 Outline of historical and palaeolimnological events at Blackbrook Reservoir. Tentative dates have been determined on the assumption of a constant sedimentation rate of 0.45 cm per year.

were not seen again as development progressed. A similar pattern was reported by Leitão & Léglize (2000) in Vieux-Pré reservoir in northeast France. In the urban reservoir Ford Lake, Michigan, USA, Donar *et al.* (1996) recorded a pulse of a related taxon, *Diatoma vulgaris* during the initial phase of reservoir development. They attributed this pulse to the creation of the reservoir producing a large body of water enriched with nutrients from newly submerged soil and decaying plant material. Blackbrook's initial phase of development (42.5-38.0 cm) can therefore be explained both in terms of available diatom inocula and ambient nutrient ratios.

As the initial pulse of nutrients was depleted and more Si was washed in from the catchment, so those taxa with higher Si:P requirements i.e. *A. formosa*, *F. crotonensis* and *A. subarctica* came to dominate Blackbrook's plankton. The wax and wane of these meso-eutrophic planktonic diatom taxa may be stochastic, simply reflecting the impact of interannual environmental variation and the seasonal growth preferences of different taxa. This steady phase in Blackbrook's history (38.0-14.0 cm) can probably be attributed to the stabilisation of Blackbrook's ecosystem and little change in the intensity of catchment land use and stream inputs. This most likely dates to the early to mid 20th century, within the period ~1915-1970.

From 14.0 cm depth, *A. islandica* begins to appear in increasing percentage relative abundance, peaking at around 6.5 cm. This results in an increase in DI-TP from ~50 μgl^{-1} to ~100 μgl^{-1}. In other studies, an increase in the percentage relative abundance of *A. islandica* in core sequences, or its appearance and subsequent increase in long-term phytoplankton records, has generally been interpreted as a sign of increasing trophic state. For example, long-term phytoplankton records from Lake Windermere (Reynolds & Irish, 2000) show that in 1965 *A. islandica* was not present in the spring phytoplankton, however since the 1980s it has been occurring alongside the established populations of *A. formosa* and *A. subarctica* as a seasonally numerous species. *A. islandica's* appearance in Lake Windermere appears to follow enhanced nutrient loadings from sewage effluent input. Canter & Haworth (1991) observe that new taxa can only invade successfully when nutrient levels are suitable and niche space is available. They suggest that *A. islandica* is able to compete with established populations because it is able to grow better in eutrophic waters. In the Laitialanselka basin of Lake Vesijärvi in Southern Finland, recent increases in sediment TP appear to be correlated with an increase in percentage relative abundance of *A. islandica*. Liukkonen *et al.* (1993) interpreted this change as reflecting an increase in eutrophication. In Lake Päijänne in Southern Finland, Meriläinen *et al.* (2001) found a two-to-three fold increase in *A. islandica* immediately after the onset of eutrophication. Prior to *A. islandica's* increase, the lake received effluent from a pulp-mill, making the water turbid and restricting the illuminated layer. After decommissioning of the pulp-mill, light penetration increased, enabling a rapid explosion of algal species, including *A. islandica*, that were best able to utilise the high available P concentrations. The onset and marked increase of *A. islandica* in Blackbrook is therefore attributed to an increase in available nutrients, which may have entered the reservoir from the increasing number of septic tanks which have accompanied

rural development within the catchment (Ian Evans, English Nature, pers. comm.). This most likely dates to the period ~1970-1985.

Lund (1950) reported that the size of the spring diatom bloom attainable is dependent upon the concentration of Si in the water column. However, although Si sets a capacity limitation on the size of the spring diatom bloom, the rate of its attainment is controlled by the availability of P (Hughes & Lund, 1962; Reynolds & Irish, 2000). Thus, P enrichment results in more rapid Si depletion and thus earlier exhaustion of Si (Reynolds, 1990; Reynolds & Irish, 2000). The initial explosion of *A. islandica* populations in Blackbrook is accompanied by both increasing diatom cell concentrations and biovolumes (Figure 8.5). Subsequently, however, cell concentrations decrease, followed by a reduction in biovolumes, perhaps reflecting depletion of Si in the water column. This observation is supported by the size and structure of *A. islandica* valves becoming finer towards the core top. In the surface sediments in particular, valves were often found to be longer and narrower and more delicate (i.e. less silicified) than in Blackbrook's earlier history (Chapter 5). Furthermore, Stoermer *et al.* (1985) and Turkia & Lepistö (1999) consider that the phenomenon of morphological variation in *A. islandica*, can be attributed to increased P loadings and subsequent Si depletion as frustules become more delicate. In Blackbrook this is supported by consistently plentiful supplies of available P observed throughout the year but seasonally low Si concentrations (Figure 6.1).

The correlation between Si and the dominance of specific diatoms is used by Kilham (1971) to predict the successional sequence of eutrophic planktonic diatoms. As Si:P ratios decrease, so taxa with lower Si requirements are favoured. This theory is observed in practice through the decreasing percentage relative abundance of *A. islandica* (high Si:P taxon) being superceded by increasing percentages of *S. parvus*, *S. neoastraea*, *C. meneghiniana* and *A. normanii* fo. *subsalsa* (low Si:P taxa) towards the core top. *A. formosa* (moderate Si:P taxon - Kilham, 1971) blooms in the spring alongside *A. islandica*, and the increasing relative abundance of *A. formosa* in relation to *A. islandica* throughout zones B-6 and B-7 could reflect its lower requirement for Si and hence its competitive advantage over *A. islandica* in the vernal period. *A. formosa* is an 'annual' (R-strategist - Reynolds, 1984b) diatom taxon that relies on a rapid rate of growth to re-establish populations under moderate Si:P conditions (Lund, 1950; Tilman, 1977; Reynolds & Irish, 2000). When the critical growth rate-limiting conditions (i.e. temperature and light) become favourable in the spring, and in the presence of sufficient P, *A. formosa* is better able to rapidly strip the water column of its reserves of Si (Hughes & Lund, 1962), concentrations of which are restored

over the winter from mixing and catchment inwash (Lund, 1950). *A. formosa* has a greater doubling-rate than *A. islandica* (Reynolds & Irish, 2000) which therefore leaves the slower growing, higher Si demanding taxon *A. islandica* with little available Si with which to establish a bloom itself. In Blackbrook *A. subarctica* shows a corresponding decrease in percentage relative abundance. It was observed by Lund (1965) that *A. subarctica* might also require higher Si concentrations than *A. formosa*. The spring-blooming taxon, *S. parvus* also increases in relative abundance at the expense of *A. islandica* in zone B-6. This may be explained by its high P demand and lower optimum Si:P ratio since Tilman *et al.* (1982) and Lynn *et al.* (2000) reported that a morphologically similar small centric taxon, *Stephanodiscus minutulus* (Grun.) was a physiologically low Si:P specialist.

The change between diatom zones 5 and 7 towards significant populations of the summer blooming taxa *S. neoastraea*, *A. normanii* fo. *subsalsa*, *C. meneghiniana* and *T. pseudonana* may be attributed to further eutrophication of Blackbrook reservoir from ~1990 to the present day. The large centric taxa, *S. neoastraea*, *A. normanii* fo. *subsalsa* and *C. meneghiniana* are *k*-strategists (slow growing and stress tolerant) (Reynolds, 1984b) with a competitive advantage at low Si concentrations and Si:P ratios (Kilham, 1971). In the London reservoir, Barn Elms No. 8, Gardiner (1941) noted that a large *A. formosa* maximum was replaced by an even larger maximum of *S. astraea* as the silica concentration fell to <1 mgl^{-1}. Alongside increasing P concentrations, dissolved ion concentrations may have also increased, further supporting the growth of pollution-tolerant taxa. *A. normanii* fo. *subsalsa* is described by Hustedt (1930) and Kiss *et al.* (1990) as being widely distributed in European eutrophic estuaries. Stoermer *et al.* (1987) reported that modern distributions of this taxon are restricted to the most eutrophic areas of the Great Lakes. They also observed that the growth requirements of *A. normanii* fo. *subsalsa* are satisfied in regions receiving relatively large nutrient and conservative ion loadings. *C. meneghiniana* was reported to be amongst the most abundant taxa in eutrophic and hypertrophic southeast Australian water storages (Tibby, 2004). Round (1998) reports that pollution by industrial and agricultural input of salts results in the increased contribution of *C. meneghiniana* to the diatom flora, indicating a positive requirement for salt. Cells of *C. meneghiniana* in Blackbrook's surface sediments are particularly large, much larger than those in Blackbrook's earlier history, and of similar morphology to those illustrated by Håkansson & Korhola (1998) from Töölö Bay, Helsinki that occurred during a period of heavy sewage pollution. Thus the cells of *C. meneghiniana* found in Blackbrook's surface sediments could tentatively be interpreted as a form of *C. meneghiniana* adapted to highly nutrient-rich and/or extreme environmental conditions. There are a number of silage pits and septic tanks within Blackbrook's

catchment (Ian Evans, English Nature, pers. comm.) and it is possible that either a slow, sustained seepage of this effluent, or perhaps more recently an isolated pollution episode, has led to the observed changes in Blackbrook's diatom populations and the increasing trend in its DI-TP.

Destratification equipment was installed at Blackbrook in approximately 1990 (John Smith, STW, pers. comm.). The absence of an accurate chronology for core BBK00C means that it is unclear whether the introduction of destratification had any influence on the initial increase in *A. islandica* or the subsequent switch from *A. islandica* to other taxa with high TP optima (i.e. *S. neoastraea, C. meneghiniana* and *A. normanii* fo. *subsalsa*). However the latter appears more likely, since analysis of a sediment core taken from Blackbrook by Sayer (unpublished) in 1990, showed that *A. islandica* was present at 30-40% relative abundance from 0 cm to a depth of 8 cm. This indicates that the expansion of *A. islandica* pre-dated the installation of destratification equipment. The recent increase in the summer blooming *S. neoastraea, C. meneghiniana, A. normanii* fo. *subsalsa* and *A. granulata* in zone B-6, may be partially explained by increased turbulence of the water column in the summer due to artificial destratification and the resuspension of resting cells (Stoermer *et al.* 1987; Sicko-Goad *et al.*, 1989). Harris *et al.* (1983) describes *S. astraea* as a 'meroplankter', whose seasonal cycle depends on a benthic reservoir of cells and periodic resuspension for survival. Similarly, both *S. astraea* and *A. granulata* are described as taxa requiring mixing of the water column to avoid losses due to rapid sedimentation of heavy cells (Lund, 1950; Moss, 1969; Kilham, 1971; Gomez et al., 1995; Tibby, 2000). Stoermer *et al.* (1987) report that *A. normanii* fo. *subsalsa* is common in shallow areas of the the Great Lakes, where natural periodic wind mixing of the water column during summer stratification enables sufficient silica to be entrained into the epilimnion to satisfy growth requirements. The switch from *A. islandica* to *S. neoastraea, A. granulata, C. meneghiniana* and *A. normanii* fo. *subsalsa* is not combined with a change in DI-TP, which remains high. This suggests that factors aside from nutrients are responsible for the observed species shift. The change of taxa does however lead to a decrease in DI-Chla, as the latter species have lower Chla optima than *A. islandica.* This may suggest that the influence of artificial aeration is the driver of the switch, since destratification has been shown to reduce overall phytoplankton biomass (Oskram and van Breeman, 1992). This may indicate that destratification is limiting algal productivity, whilst nutrient loadings have been maintained at high levels, since DI-Chla increases but DI-TP remains stable.

When Si becomes depleted, diatoms usually become scarce and are ultimately replaced or superseded in biomass by non-siliceous algae (i.e. chlorophytes and cyanophytes) (Kilham, 1971; Sommer, 1989). This is observed over the late summer period in Blackbrook and in many other eutrophic reservoirs in the current study. However the presence of taxa such as *S. neoastraea* and *A. normanii* fo. *subsalsa* are recorded during this period. Since the cyanophyte blooms (*Microcystis* spp.) seen in Blackbrook reservoir are redistributed throughout the water column by artificial aeration, water clarity remains moderate (but lower than in the spring). Moderate water clarity is possible because light can penetrate between individual algal colonies to a depth of ~1.5 m, in turn enabling the growth of the *k*-strategists, *S. neoastraea* and *A. normanii* fo. *subsalsa*. In response to eutrophication, larger cells gain a competitive advantage over smaller cells due to high nutrient availability but a reduction in the solar energy available at high algal biomass (Harris *et al.*, 1983). In Hamilton Harbour, Lake Ontario, Harris *et al.* (1983) reported that periods of mixing favoured algae of "large" size classes such as *S. astraea*, whereas stable periods were dominated by taxa of "small" or "medium" size. This was explained by the higher apparent quantum efficiencies of the larger cells. Perturbation of the mixed layer depth of Blackbrook reservoir, due to artificial destratification, is therefore thought to have influenced the recently observed change in phytoplankton community composition and biomass (Reynolds, 1980).

At the time of SSSI notification in 1985, Blackbrook was described as a 'mesotrophic' site. Although the site can still be classified as 'mesotrophic' in terms of Chla (current measured Chla = 6 μgl^{-1} and DI-Chla = 5.3 μgl^{-1}) and TP concentrations indicate that it is 'hypertrophic' (current measured TP and DI-TP ~120 μgl^{-1}). Carvalho & Moss (1995) did not report any change in Blackbrook's conservation interest since SSSI notification in 1985, but it was recommended that further investigation should be carried out. In 2001, English Nature classified Blackbrook's condition as "unfavourable declining", supporting the conclusions of the current study, that Blackbrook's water quality has deteriorated since its SSSI designation in 1985. The observations made in this study suggest that it is the combined influence of both chemical and physical factors that have led to the observed changes in Blackbrook's diatom populations. It appears that nutrient enrichment instigated the initial increase of *A. islandica*. Subsequent to this, the nutrient status has stabilised or increased only slightly, but other factors have led to a switch from *A. islandica*, to *A. formosa* and *S. parvus* in the spring and to *S. neoastraea*, *C. meneghiniana,* and *A. normanii* fo. *subsalsa* in the summer. Limitation of Si, particularly in the spring, may have caused

this shift. In combination with the installation of destratification equipment, this has given the summer-blooming diatom species a competitive advantage over *A. islandica*.

Blackbrook's diatom stratigraphy and DI-TP reconstruction indicates relatively stable mesotrophic conditions prior to ~1970 (zones B2-B3). This period may therefore provide an analogue restoration target to inform management decisions relating to the reservoir's recovery from its present hypertrophic state.

8.4 Daventry reservoir

8.4.1 Background information

Daventry Reservoir in Northamptonshire (OS grid ref SP580640) is owned by the British Waterways Board (BWB) and was constructed in 1804 as a canal feeder reservoir for the Grand Union Canal. When filled to maximum capacity, the reservoir covers an area of ~28 ha and has a maximum depth of 10 m, although a depth of only 7 m was recorded during sampling in May 2000. The reservoir is located within the Daventry Country Park (DCP) (~57 ha in area), which is owned and managed by Daventry District Council (DCC) for public access and conservation (Daventry District Council, undated).

Site History

A sewage works was constructed at the site during the 1890s. This processed Daventry's sewage until 1974 when it was decommissioned. However it was not fully dismantled at this time and sludge lagoons remained. The land comprising the old sewage works was finally decontaminated and the land reclaimed in 1992, with reed beds planted on the site of the former sludge lagoons. Several pollution episodes have been reported, including the release of several thousand gallons of heating oil from the 'Ford' industrial plant during the 1970s (Dewi Morris, DCP, written comm.).

In an attempt to limit, intercept and control the amount of pollution entering the reservoir, a grit trap was installed at the inflowing (southern) end of the reservoir during the winter and spring of 1972-73 (Figure 8.9b; Dewi Morris, DCP, written comm.). The grit trap is reported to have been emptied on a least three occasions; twice since 1973 and once in 1997 (Dewi Morris, DCP, written comm.). An oil trap was also installed at the same time as the grit trap with the purpose of intercepting sludge wastes. The reservoir itself was last dredged in the early 1900s (M. Judd, BWB, pers. comm.). Therefore, the reservoir was thought to

provide a 'good' sequence of sediments from which to analyse and reconstruct past environmental changes.

Geology and soils

The geology of the area consists predominantly of base-rich sedimentary rocks comprising clays, mudstones, sandstones and silts of the Lower Jurassic Middle Lias (sandy siltstone and silty mudstone with ferruginous concretions). The hills bordering the south and east of Daventry reservoir's catchment consist mainly of heavy Upper Lias clay (bluish grey mudstone with fine-grained sand), capped on the top by Northampton Sand (ironstone and ferruginous sandstone). A band of Marlstone (ferriginous limestone and sandstone with ironstone) occurs in outcrops along the lower slopes of the hills.

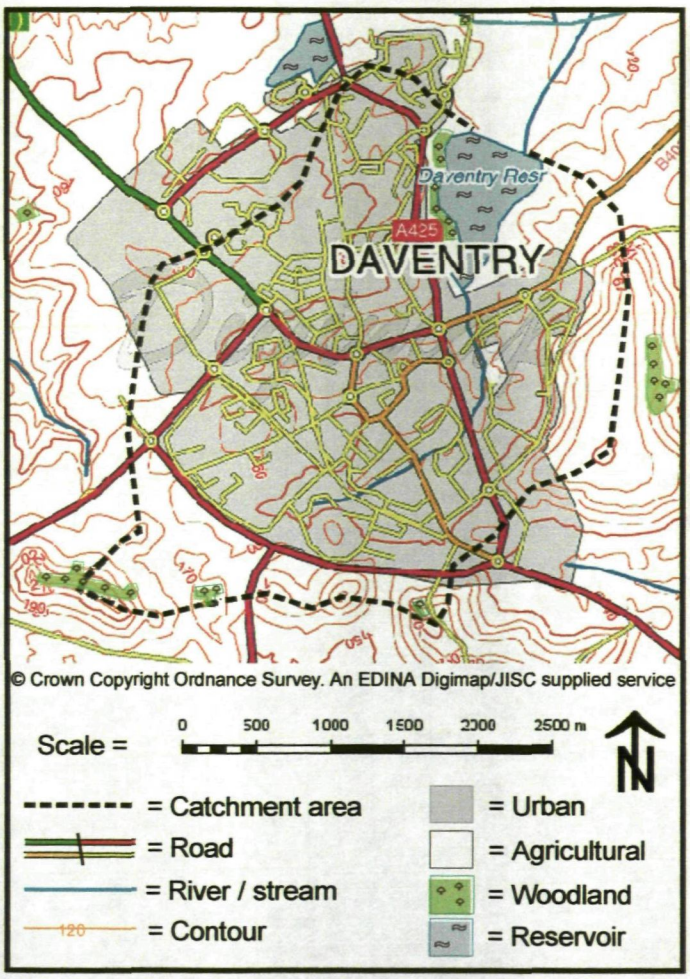


Figure 8.8 Catchment area and land use map for Daventry reservoir

Catchment land use

Figure 8.8 illustrates the extent of Daventry Reservoir's catchment and highlights the predominantly urban land-use. Since the reservoir's construction, the town of Daventry has increased considerably in size. Between 1841 and 1951 the population remained relatively

stable at around 4000 people. By 1971 this had risen to 12000 and by 1991 the population had further increased to 18000 (Greenall, 1999). When Daventry reservoir was constructed, the percentage of urban land use in its catchment was ~10%, with the remainder comprising agricultural land (Greenall, 1999). Land use in the catchment remained relatively constant until the expansion of the town and its population in the latter half of the 20th century. The reservoir's catchment now comprises ~80% urban land use and contains many features of the urban environment (e.g. housing, schools). Of particular note are the presence of engineering works and industrial estates, particularly in the western sector of the catchment. There are numerous roads and bypasses located in the reservoir catchment and runoff from these is ultimately deposited in the reservoir. Several small streams also feed the reservoir.

Conservation interest

The reservoir is fringed by a range of wetland habitats in turn surrounded by areas of woodland and grassland with mature hedgerows. The park supports many floral and faunal species and is an important area of countryside located in a predominantly urban environment. A nature reserve is located to the south of the reservoir within the DCP.

Reservoir water levels drop markedly throughout the summer and autumn. The exposure of mud as the water recedes is important for wildlife, particularly plants, supporting six species rare to Northamptonshire. Mudwort, *Limosella aquatica* is one of these rarities, a native species found only in scattered localities throughout Britain and Ireland (Stace, 1999). It grows on the mud in profusion as reservoir levels fall. The muddy shoreline also attracts large numbers of wildfowl and wading birds, some of which (including Great-crested grebe) breed at the site (Daventry District Council, unpublished).

8.4.2 Daventry's sedimentary record

Coring locations (DAV00F, DAV00A and DAV00G)

Figure 8.9b illustrates the locations of the nine sediment cores retrieved from Daventry reservoir. Only cores A, F and G are referred to in this chapter.

Cores DAV00A and DAV00F were extracted from an area of potential sediment focussing in relatively close proximity to the dam wall, but of sufficient distance from this feature to avoid possible sediment re-working and turbulence. These cores were utilised for lithostratigraphic and diatom analyses respectively, and core DAV00F was dated using ^{137}Cs. Core DAV00G was extracted from a mid-reservoir location and was used as the master core. It was analysed for geochemistry and was dated using both ^{210}Pb and ^{137}Cs. For

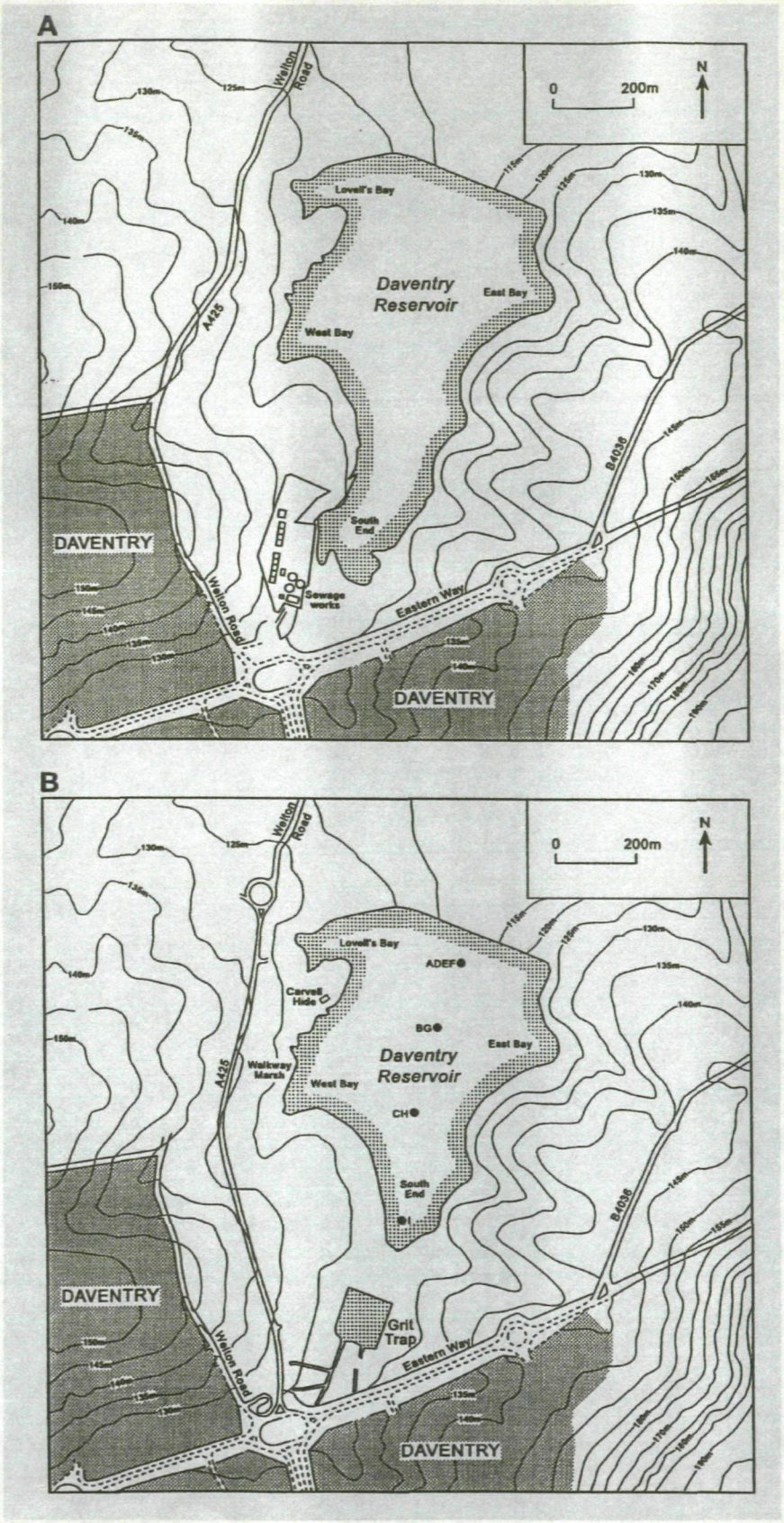


Figure 8.9 **(A) Map of Daventry reservoir as it appeared pre-1970. (B) Daventry reservoir as it appears today, following grit-trap installation (1972/3), and sewage works decommissioning (1974) and reclamation (1992). Also shown are the locations of the nine sediment cores retrieved (A-I), although only cores A, F and G are referred to in this chapter.**

the most part, the sediment from core DAV00F is used to provide the data from which the results presented in this section are derived. Where data are derived from other cores, this is highlighted in the text.

Sediment lithology

DAV00F was one of nine sediment cores retrieved from Daventry Reservoir (see Figure 8.9b for coring locations). The sediments of all cores comprised mostly brown fluid lake muds (the upper ~6 cm) to black organic-rich lake muds (Table 8.6).

Depth (cm)	Description
0-6	Brown fluid lake mud
6-46	Black organic-rich lake mud

Table 8.6 Sediment lithology of core DAV00F

DAV00F represents the period in Daventry's history subsequent to sediment removal in the early 1900s. Thus the sediment sequence does not span the entire history of the reservoir, since the oldest sediments dating back to the reservoir's inauguration in 1804 have been removed by dredging. Dating results presented below will shed light on the chronology and time period represented by DAV00F.

Lithostratigraphy

%DW, %LOI and $\%CaCO_3$ were determined only for core DAV00A (Figure 8.10). Because this core was taken in a similar location to DAV00F and both sediment depth and lithology are comparable between cores, it is assumed that the lithostratigraphic profiles of DAV00A and DAV00F will also show similar trends.

%LOI is more or less steady at ~15% between the core base (43 cm) and ~28 cm. Above ~25 cm depth (~AD1964), it decreases and remains relatively stable at ~12-13% until the core top. This indicates that the organic matter content of Daventry's sediments has decreased from ~AD1964 to the present day, possibly reflecting progression towards less productive conditions in the reservoir.

$\%CaCO_3$ is considerably higher in Daventry than in Blackbrook (~30% compared with ~10%), probably reflecting differences in catchment geology. The profile shows values of 30% at the core base (43 cm), then between 40.5-32.5 cm values decrease to 21-23%, before steadily increasing again to ~35% between 28.5-1.0 cm. In the uppermost sediments (0-1

cm), a small increase in $\%CaCO_3$ occurs to 32%, but the reason for this is uncertain. The relatively high $\%CaCO_3$ is thought to be closely related to Daventry's base-rich catchment geology and inwash. This is supported by the lack of evidence for significant internal biological sources of $CaCO_3$, such as the presence of charophytes (cf. Blackbrook: section 8.3.)

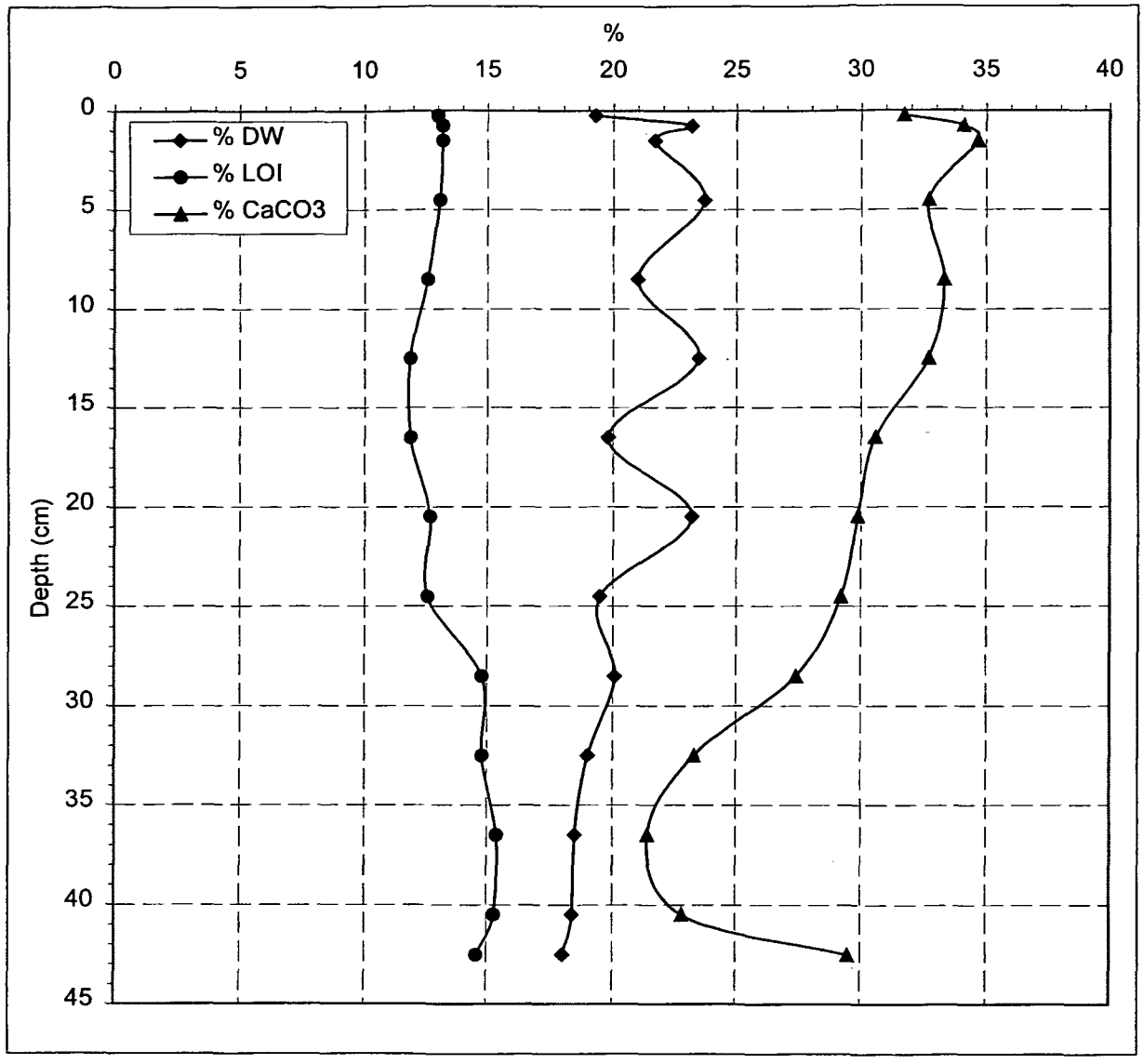


Figure 8.9 Sediment lithostratigraphy for core DAV00A, illustrating percentage dry weight (%DW), percentage organic matter (%LOI) and percentage calcium carbonate ($\%CaCO_3$).

Dating of Daventry's sediments

The master core, DAV00G, was dated using both the ^{210}Pb and ^{137}Cs radionucleides (results not presented here – see Eastwood *et al.*, 2002 for details). For DAV00G, the ^{137}Cs peaks correspond to the ^{210}Pb ages for the same horizons, suggesting good correlation of the two dating methods. Therefore core DAV00F was dated using only the ^{137}Cs method (see Chapter 3 for details).

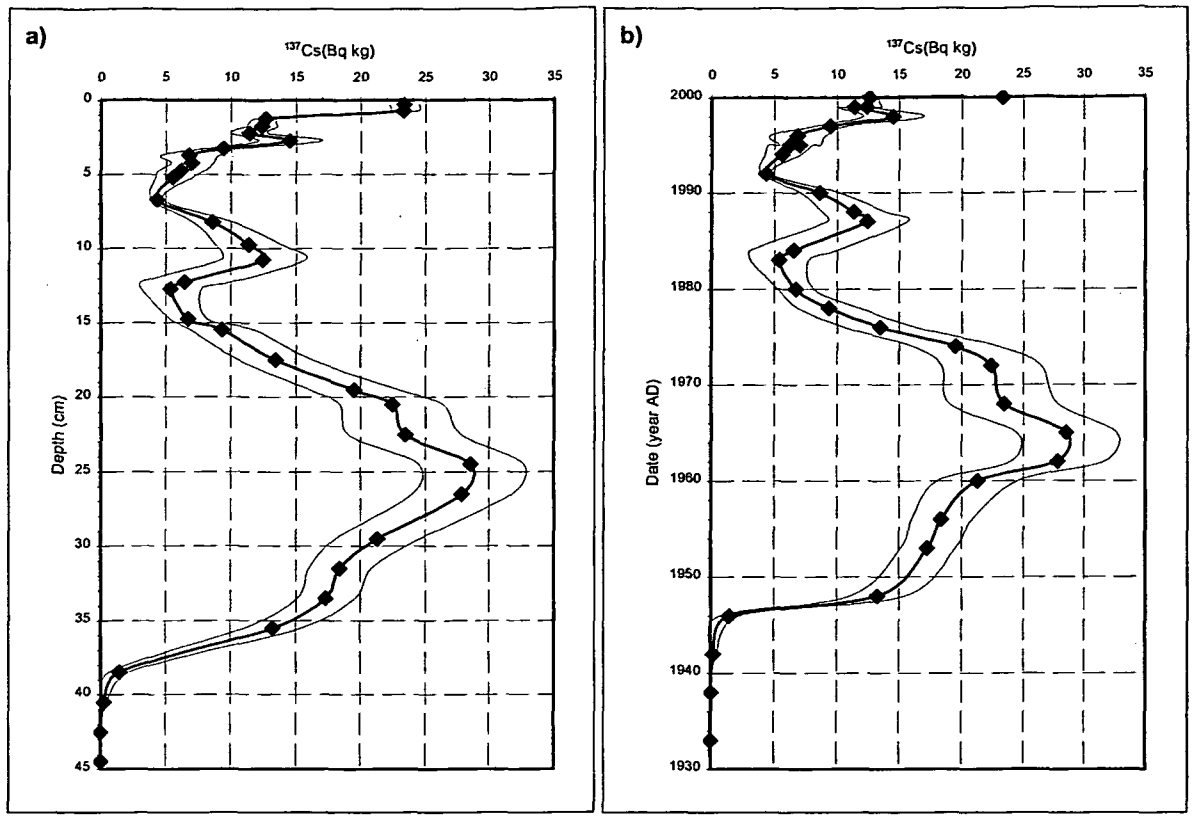


Figure 8.10 **^{137}Cs content for core DAV00F plotted against a) depth and b) date. Errors associated with the dates are plotted.**

Figure 8.11 **Age vs. depth curve for core DAV00F plotted against years before 2000 (Ages determined by ^{137}Cs dating methods). A linear trend-line is fitted and errors associated with the dates are plotted.**

Sample depth (cm)	^{137}Cs (Bq kg) ± error	Age (years before 2000)	Year of deposition ± error	Interpretation
0.25	23.33 ±1.12	0	2000 ±4.6	Re-working of
1.25	12.64 ±0.85	0.3	1999.7 ±4.5	older sediments
3.25	9.46 ±1.32	3	1997 ±5.3	
5.25	5.64 ±1.43	6	1994 ±4.5	
6.75	4.35 ±0.45	8	1992 ±3.4	
7.25		9	1991 ±4.7	
8.25	8.65 ±1.54	10	1990 ±4.7	
9.25		11	1989 ±6.3	
9.75	11.34 ±2.54	12	1988 ±6.3	Chernobyl peak
10.75	12.43 ±3.22	13	1987 ±6.3	(1986)
11.25		14	1986 ±6.3	
12.25	6.54 ±3.45	16	1984 ±5.8	
12.75	5.43 ±2.34	17	1983 ±5.0	
13.25		18	1982 ±6.2	
14.75	6.76 ±1.43	20	1980 ±6.2	
15.5	9.35 ±2.43	22	1978 ±6.9	
17.5	13.45 ±2.87	24	1976 ±7.2	
18.5		25	1975 ±7.2	
19.5	19.54 ±3.43	26	1974 ±7.0	
20.5	22.43 ±3.98	28	1972 ±7.0	
21.5		30	1970 ±7.1	
22.5	23.45 ±4.35	32	1968 ±7.1	
24.5	28.55 ±4.09	35	1965 ±7.8	'Bomb' peak from
25.5		37	1963 ±8.5	atom bomb testing
26.5	27.85 ±3.89	38	1962 ±8.5	(1963)
29.5	21.34 ±3.24	40	1960 ±8.7	
31.5	18.43 ±2.43	44	1956 ±8.3	Windscale fire
33.5	17.34 ±2.22	47	1953 ±8.2	(1957)
35.5	13.24 ±2.19	52	1948 ±8.7	
37.5		53	1947 ±8.7	
38.5	1.45 ±0.78	54	1946 ±8.2	
40.5	0.23 ±0.21	58	1948 ±9.2	
41.5		60	1940 ±9.2	
42.5	0.00 ±0.00	62	1938 ±9.2	No ^{137}Cs
44.5	0.00 ±0.00	67	1932 ±10.3	below 42 cm
45.5		69	1931 ±10.3	

Table 8.7 **^{137}Cs dating results for core DAV00F. For sample depths where no ^{137}Cs content is presented, age and year of deposition (± error) has been extrapolated. Sample depths in bold illustrate samples analysed for diatoms.**

Figure 8.12 illustrates that for core DAV00F, there is a good linear relationship between the ^{137}Cs derived age and core depth (r^2 = 0.9985). This suggests an overall constant sedimentation rate (SAR) of 0.702 cm y^{-1} (0.911 kg m^{-2} y^{-1}) for DAV00F. The ^{137}Cs profile fits the 'classical' shape of other ^{137}Cs profiles reported in the literature (see Ivanovich & Harmon, 1992 and Appleby, 2001). Table 8.7 details the ^{137}Cs dating results for core DAV00F. Where dates have been extrapolated (for some samples analysed for diatoms), a constant sedimentation rate has been assumed. Since there is no ^{137}C detectable below a depth of 42 cm, linear extrapolation was used to derive a date of 1931 ± 10.3 years for the base of the core (45.5 cm). Absence of ^{137}C below 42 cm provides evidence that there is no down-core ^{137}Cs mobility. The ^{137}Cs detected in the uppermost layers of the core appear to

be sediment-bound and have probably resulted from the re-working of older sediment sources. DAV00F represents sediments deposited from the 1930s to 2000 and the core does not extend back to the date the reservoir was constructed (1804). Overall, the dating profile for core DAV00F is of high quality, providing a robust chronological framework with which to date key events in the palaeoenvironmental record. The errors in the dating method associated with each derived date range from ±3 to ±10.3 years, generally increasing down core. These should be taken into consideration when interpreting the timing of key events in Daventry's history.

8.4.3 Daventry's diatom stratigraphy

Table 8.8 and Figure 8.13 show that diatom cell concentrations and biovolumes follow a very similar stratigraphic trend in DAV00F. On occasions where biovolumes are lower than cell concentrations, smaller taxa with low biovolumes are dominant e.g. *S. parvus* (108 μm^3), *A. granulata* var. *angustissima* (302 μm^3), *C. dubius* (523 μm^3) and *A. ambigua* (618 μm^3). Where biovolumes are higher than cell concentrations, large-celled taxa with correspondingly large biovolumes are dominant e.g. *C. meneghiniana* (5429 μm^3), *S. hantzschii* fo. *tenuis* (4181 μm^3) and *Stephanodiscus hantzschii* (1608 μm^3).

At the base of core DAV00F both diatom cell concentrations and biovolumes are low (~50 cells g^{-1} DW $x10^6$ and ~50 μm^3 g^{-1} DW $x10^9$). In the middle of the core at 25.5-11.25 cm depth, both cell concentrations and biovolumes are high and fluctuating (100-150 cells g^{-1} DW $x10^6$ and 100-200 μm^3 g^{-1} DW $x10^9$). At the core top (9.25-0.25 cm), both cell concentrations and biovolumes steadily return to levels recorded at the base of the core. This probably indicates that Daventry reservoir has become less productive in recent years.

DAV00F is dominated by planktonic centric diatoms (>90% abundance). The paucity of periphytic diatom taxa suggests that the photic zone does not reach the bottom of the reservoir. A mean secchi depth of 2 m was recorded during this study; therefore the photic zone would not be expected to extend to more than ~5 m depth for most of the year, which is less than the maximum depth of the reservoir. The main diatom habitat is in the plankton, and it is the planktonic diatom taxa that experience the greatest fluctuations throughout DAV00F.

Sample depth (cm)	Total number of taxa	Total valve count	Floristic diversity	Diatom concentration Aliquot method (cells g^{-1} DW $x10^6$)	Diatom biovolume (μm^3 g^{-1} DW $x10^9$)
0.25	42	475	0.09	59.69	63.50
1.25	26	290	0.09	42.53	48.86
3.25	41	442	0.09	56.36	62.58
5.25	39	460	0.08	85.60	85.63
7.25	37	451	0.08	95.42	84.06
9.25	31	471	0.07	80.13	110.46
11.25	38	412	0.09	139.92	169.38
13.25	37	394	0.09	111.76	108.05
15.50	41	412	0.10	149.88	199.30
18.50	35	369	0.09	121.08	88.79
21.50	37	327	0.11	138.68	135.82
25.50	30	329	0.09	112.24	80.11
29.50	27	361	0.07	44.97	89.38
33.50	22	342	0.06	216.54	149.74
37.50	23	298	0.08	51.75	123.85
41.50	21	257	0.08	41.52	65.48
45.50	15	313	0.05	52.78	45.34
Mean	32	377	0.08	94.17	106.49
Median	35	369	0.09	85.60	89.38
Min	15	257	0.05	41.52	45.34
Max	42	475	0.11	216.54	199.30
SD	8	69	0.02	48.59	46.84

Table 8.8 **Diatom cell concentrations, counts and diversity statistics for core DAV00F**

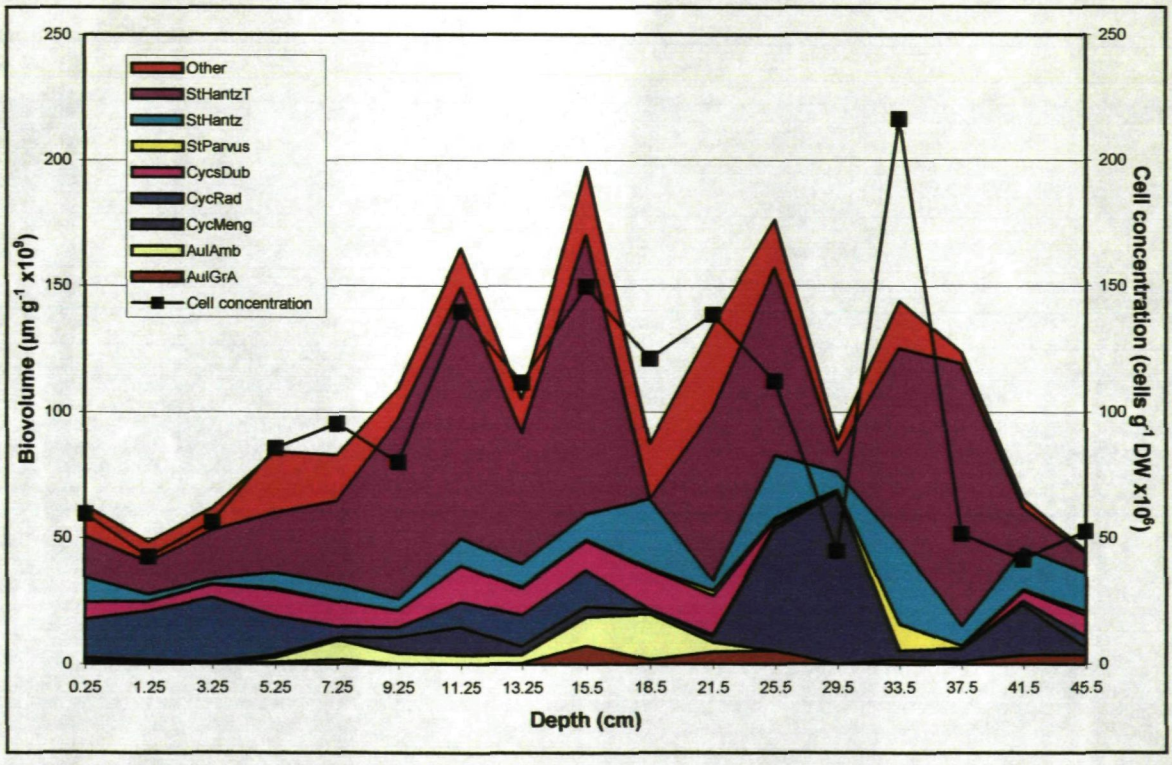


Figure 8.13 **Diatom cell concentrations (determined by the aliquot method) and cell biovolumes plotted against depth for core DAV00F. (Note that the depth scale is not regularly spaced and is related to sample number).**

Figure 8.14 illustrates the summary diatom data for core DAV00F. Only the 21 taxa occurring at ≥3% relative abundance in one or more samples are presented. Illustrated alongside are the overall percentages of planktonic/periphytic taxa and the diatom cell concentrations and biovolumes. Also shown are diatom-inferred TP, Chla and EC reconstructions using the full model, which are discussed in section 8.4.4.

The diatom data for core DAV00F (Figure 8.14) are divided into 6 diatom assemblage zones (D-1 to D-6). Zone boundaries were determined (as described for BBK00C in section 8.3.3) for all diatom taxa in the 17 sample levels. In stratigraphic order, the zone boundaries are 39.5 cm, 35.5 cm, 23.5 cm, 17.0 cm and 6.25 cm. An age scale based upon the linear interpolation (and extrapolation) between adjacent radiometric ages produces ages of 56 BP (1944 ± 9.2), 52 BP (1948 ± 8.7), 33 BP (1967 ± 7.8), 24 BP (1976 ± 7.2) and 7 BP (1993 ± 4.5) respectively for the above zone boundaries.

Zone D-1, 45.5-39.5 cm, 69-56 yrs BP (AD 1931-1944):

The base of zone D-1 records the presence of *Cyclostephanos dubius* (30-20%), *S. parvus* (30-15%) and *C. meneghiniana* (~10%). Also present are *C. radiosa* (5%), *Cyclostephanos* cf. *tholiformis* (~4%) and *A. granulata* (5%). *S. hantzschii* fo. *tenuis* and *Stephanodiscus hantzschii* both record increases throughout zone D-1, with *Stephanodiscus hantzschii* occurring at a higher percentage relative abundance (~20%). Zone D-1 is interpreted as a period in the reservoir's history when eutrophic conditions prevailed, with the occurrence of *C. radiosa* indicating that taxa favouring mesotrophic conditions were able to survive. Diatom cell concentrations are at their lowest and most stable in zone D-1 (40-50 $x10^6$ cells g^{-1} DW), whereas biovolumes are increasing (from 45 to 65 $x10^9$ μm^3 g^{-1} DW).

Zone D-2, 39.5-35.5 cm, 56-52 yrs BP (AD 1944-1948):

Zone D-2 is dominated by *S. hantzschii* fo. *tenuis* (48%). *C. dubius* decreases markedly to 3%. *Stephanodiscus hantzschii* continues to occur, although at lower percentage values than in the previous zone (10%), whereas *S. parvus* continues to occur at similar values to those seen in D-1 (14%). The periphytic taxon *Nitzschia amphibia* occurs at its highest percentage values in this zone (5%). Zone D-2 is interpreted as a period of hypertrophy, as indicated by the high percentage relative abundance of *S. hantzschii* fo. *tenuis*. Diatom cell concentrations continue at low and stable values in zone D-2 (52 $x10^6$ cells g^{-1} DW), whilst biovolumes continue to increase (124 $x10^9$ μm^3 g^{-1} DW).

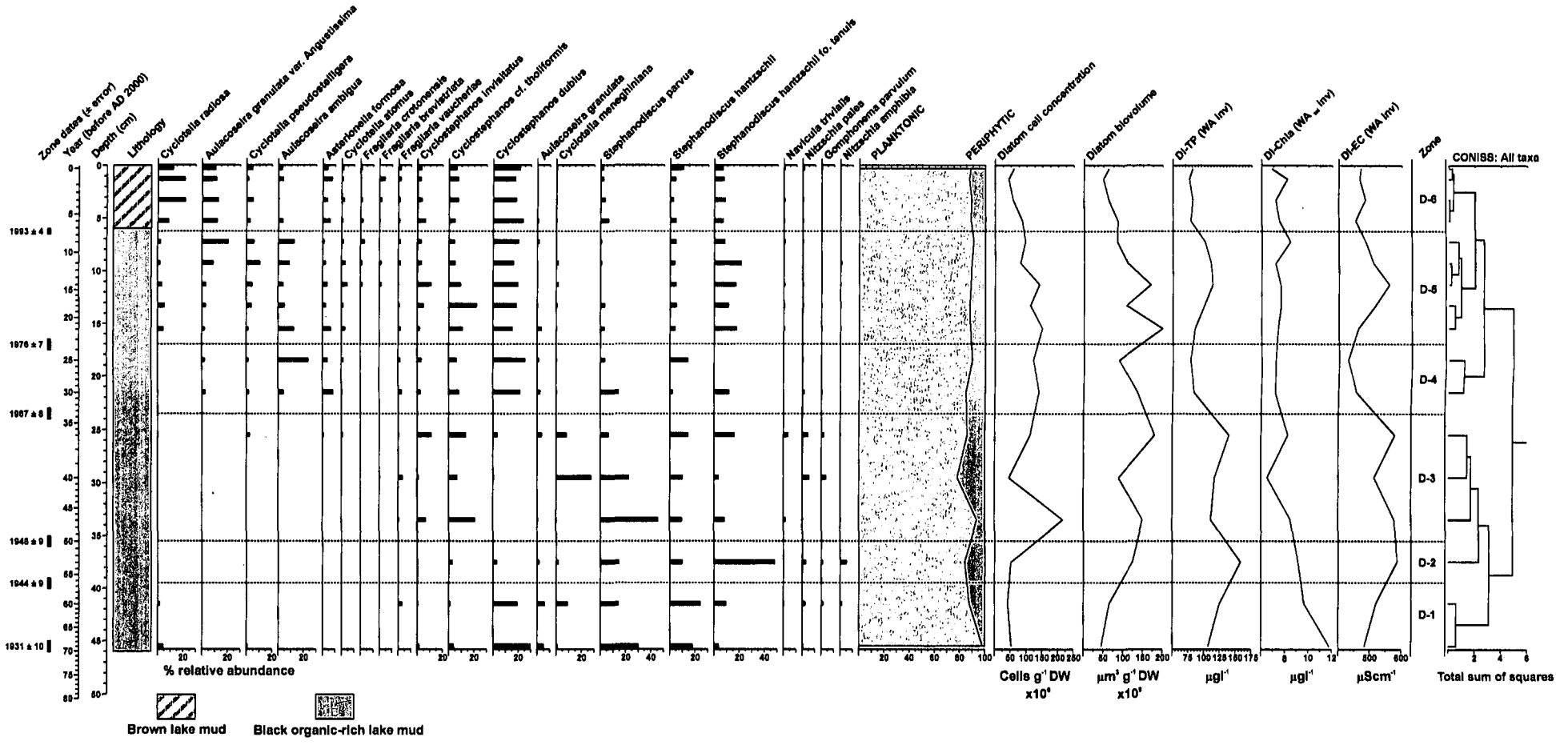


Figure 8.14 Stratigraphic profiles of the dominant species, diatom habitats, %LOI, diatom population statistics and diatom-inferred reconstructions (full model) in DAV00F (only taxa occurring with ≥3% abundance in one or more samples are shown).

Zone D-3, 35.5-23.5 cm, 52-33 yr BP (AD 1948-1967):

Zone D-3 shows some important changes in diatom taxa, namely a marked decrease in *C. dubius* to trace percentage values and a decrease in *Stephanodiscus hantzschii* and *S. hantzschii* fo. *tenuis* to less than 10%. These decreases are mirrored by increases in *Cyclostephanos invisitatus* (10%), *C.* cf. *tholiformis* (20%), *C. meneghiniana* (28%) and *S. parvus* (45%). Due to significant increases in *C. meneghiniana* during zone D-3, this period is interpreted as one of hypertrophic conditions. Diatom cell concentrations reach a peak at the start of zone D-3 (217 $x10^6$ cells g^{-1} DW), and then decrease markedly, followed by a steady increase. Biovolumes follow a similar, but less accentuated trend, peaking at the top of zone D-3 (180 $x10^9$ μm^3 g^{-1} DW).

Zone D-4, 23.5-17.0 cm, 33-24 yrs BP (AD 1967-1976):

Important changes in diatom taxa are recorded during zone D-4, namely the elimination of *C. meneghiniana*, overall decreases in *S. parvus* from the previous zone, decreases in *S. hantzschii* fo. *tenuis* (~15%), *C. invisitatus* (~8%) and a slight decrease in *C.* cf. *tholiformis* (~8%). There are important appearances of *A. ambigua* (25%) and *A. granulata* and increases in *C. dubius* (~20%), *A. formosa* (~8%) and *A. granulata* var. *angustissima* (~2%), indicating a return to eutrophic conditions from the period of hypertrophy seen throughout zones D-3 and D-2. Diatom cell concentrations remain high in zone D-4 (~130 $x10^6$ cells g^{-1} DW), whilst biovolumes decrease (136-89 $x10^9$ μm^3 g^{-1} DW), probably reflecting the increasing abundance of the low biovolume taxon, *A. ambigua*.

Zone D-5, 17.0-6.25 cm, 24-7 yrs BP (AD 1976-1993):

Zone D-5 records the re-appearance (at more than just trace values) of *C. radiosa* (~5%), together with slight increases in *Cyclotella pseudostelligera* (~2-10%). Whereas there is a decrease and subsequent increase in percentage values of *A. ambigua*, percentage values for *A. formosa* decrease slightly and the relative abundance of *A. granulata* var. *angustissima* increases during D-5. *F. crotonensis* appears for the first time during D-5. Although there are short-lived peaks in *C.* cf. *tholiformis* towards the start of the zone (~25%), and *C. invisitatus* in the middle of the zone (~10%), Daventry's trophic state remains relatively constant in the eutrophic category. Diatom cell concentrations remain high at the start of zone D-5 (~145 $x10^6$ cells g^{-1} DW), decreasing towards the top. Biovolumes are high and fluctuating at the start of this zone (89-199 $x10^9$ μm^3 g^{-1} DW), and in common with cell concentrations, decrease at the top of this zone.

Zone D-6, 6.25-0.0 cm, 7-0 yrs BP (AD 1993-2000):

During zone D-6 there is a sustained increase in *C. radiosa* (8-21%), a diatom taxon indicative of lower nutrient conditions and an indicator that Daventry reservoir is perhaps moving towards a mesotrophic state. Proportions of *C. dubius* and *A. granulata* var. *angustissima* remain relatively stable and at moderate levels. *A. formosa*, *A. ambigua*, *C.* cf. *tholiformis*, *Stephanodiscus hantzschii*, *S. hantzschii* fo. *tenuis*, *C. invisitatus*, *C. pseudostelligera*, *Cyclotella atomus* and *F. crotonensis* also remain at relatively constant but low values. Both diatom cell concentrations and biovolumes decrease gradually throughout zone D-6 to their lowest levels since zone D-1 (86-42 $x10^6$ cells g^{-1} DW and 86-49 $x10^9$ μm^3 g^{-1} DW respectively).

8.4.4 Reconstructing Daventry: Diatom-inferred total phosphorus (TP), chlorophyll-*a* (Chla) and conductivity (EC) reconstructions

This section presents the results of DI-TP, DI-Chla and DI-EC reconstructions for Daventry reservoir based on the most appropriate model (WAPLS or WA/WA_{tol} using either classical or inverse deshrinking methods) for each variable (TP, Chla and EC) and for each dataset (full and plankton-only).

Choice of models for reconstructions

Table 8.9 displays both the models selected for reconstruction purposes at Daventry and the reasoning behind these choices. The models selected for TP reconstruction using both the full and plankton-only datasets are the same as those highlighted in Chapter 7 (Table 7.3) as having the lowest prediction errors. The simple WA inverse deshrinking model best predicts current TP concentrations (84 μgl^{-1}) for both datasets whereas WA_{tol} models underpredict current TP. Although some of the dominant diatom taxa show a broad tolerance to TP, many do not and thus DI-TP reconstructions for DAV00F are performed using the most robust models based on WA inverse deshrinking.

The models chosen for Chla reconstruction using both the full and plankton-only datasets employ WA_{tol} inverse deshrinking. Although tolerance-downweighted models are not as robust as those developed using simple WA (Table 7.7), the Chla trends are similar and tolerance downweighting is considered essential since most dominant taxa show broad WA derived tolerances to Chla.

The model selected for EC reconstruction using both the full and plankton-only datasets is that employing WA inverse deshrinking; the best model in terms of performance statistics

(Table 7.12). Although DI-EC for the surface sediment sample is well below current measured values (~450 μScm^{-1} as opposed to ~700 μScm^{-1}), reconstructed values are no closer to current values when the other models are employed. It is suggested that under-prediction of current EC could arise because many of the diatom taxa present in Daventry's fossil record show a poor response to EC (Figure 7.11a). An alternative explanation is that the trend in the residuals for the WA inverse deshrinking model shows inherent underprediction of EC at high levels, although it is unlikely that the extent of underprediction could explain a discrepancy of ~250 μScm^{-1}.

Variable	Choice of models for the full and plankton-only diatom inferred reconstructions	
	Full model	**Plankton-only model**
TP	**WA inverse** a) Lowest RMSEP of all models b) Surface sediment DI-TP concentration closest to current epilimnetic TP c) Most abundant and frequently occurring taxa show a range of tolerances both above and below mean values	**WA inverse** (see full model for reasoning)
Chla	**WA_{tol} inverse** a) Majority of most abundant and frequently occurring taxa have large tolerances for Chla (although this model under performs models created using simple WA)	**WA_{tol} inverse** (see full model for reasoning)
EC	**WA inverse** a) All models show similar trend in reconstructed DI-EC and all under-predict current EC values, but WA inverse shows lowest RMSEP and low mean and max bias b) Most abundant and frequently occurring taxa show a range of tolerances both above and below mean values	**WA inverse** (see full model for reasoning)

Table 8.9 Inference models selected for environmental reconstructions at Daventry reservoir and reasoning behind choices

Diatom-inferred total phosphorus reconstruction (DI-TP)

Figure 8.15a shows the DI-TP reconstruction for DAV00F according to the WA inverse deshrinking model and based on the full dataset. The SEPs (estimated by bootstrapping) show that the maximum error in the model could increase reconstructed DI-TP by a factor of two. These SEPs are comparable to those seen in BBK00C (see section 8.3.4).

The DI-TP reconstruction shows a clear overall decreasing trend from the core base (1931), to the present day. Unlike the DI-TP reconstruction profile for BBK00C, distinct phases are less apparent, although general phases are discernable.

The first phase is one of increasingly high but fluctuating DI-TP (107-158 μgl^{-1}) between 1931 and 1963. The base of the core shows a DI-TP of 107 μgl^{-1}, which rises to a peak of 158 μgl^{-1} in 1947 before falling back to 111 μgl^{-1} in 1953. It again rises to a peak in 1963 of 140 μgl^{-1}. DI-TP therefore increases from a minimum in 1931 that is on the cusp between 'eutrophic' and 'hypertrophic' (according to OECD (1982) TP criteria), fluctuating but becoming increasingly 'hypertrophic' throughout this phase.

The next phase sees a significant decrease in DI-TP between 140 μgl^{-1} in 1963 and 78 μgl^{-1} in 1975. This decrease takes Daventry out of the 'hypertrophic' and into the 'eutrophic' OECD classification throughout most of the 1970s.

The third phase shows increasing DI-TP concentrations from the late 1970s to the mid-1980s. DI-TP rises from 78 μgl^{-1} in 1975 to a peak of 113 μgl^{-1} in 1986. This peak is substantially lower than the maxima seen in 1947 and 1960, but does push the reservoir back into the 'hypertrophic' category for most of this period.

The final phase sees a further reduction in DI-TP from 113 μgl^{-1} in 1986 to a minimum of 76 μgl^{-1} in 1999, with a final reconstructed DI-TP concentration of 82 μgl^{-1} in 2000. This compares well with the current mean annual TP of 84 μgl^{-1} measured in this study. This final phase shows that from the early 1990s Daventry's trophic status lies well within the 'eutrophic' category according to OECD (1982) TP criteria.

The plankton-only model DI-TP trend generally follows a similar pattern, with comparable reconstructed values to those seen under the full model (Figure 8.15b). It does, however, show a different trend for the first phase of DAV00F from 1931 to 1963. Whilst DI-TP does fluctuate during this period, the plankton-only model appears to show an overall trend of increasing DI-TP during this phase. In 1931 the plankton-only model reconstructs a DI-TP concentration of <100, 'eutrophic' according to the OECD criteria. Each decade from the 1930s to the 1950s ends with higher TP than it started, with an absolute peak in the plankton-only model DI-TP concentration in 1960, contrasting with the full model's DI-TP peak dated to 1947. From 1960 onwards, the reconstructions derived from the two models converge.

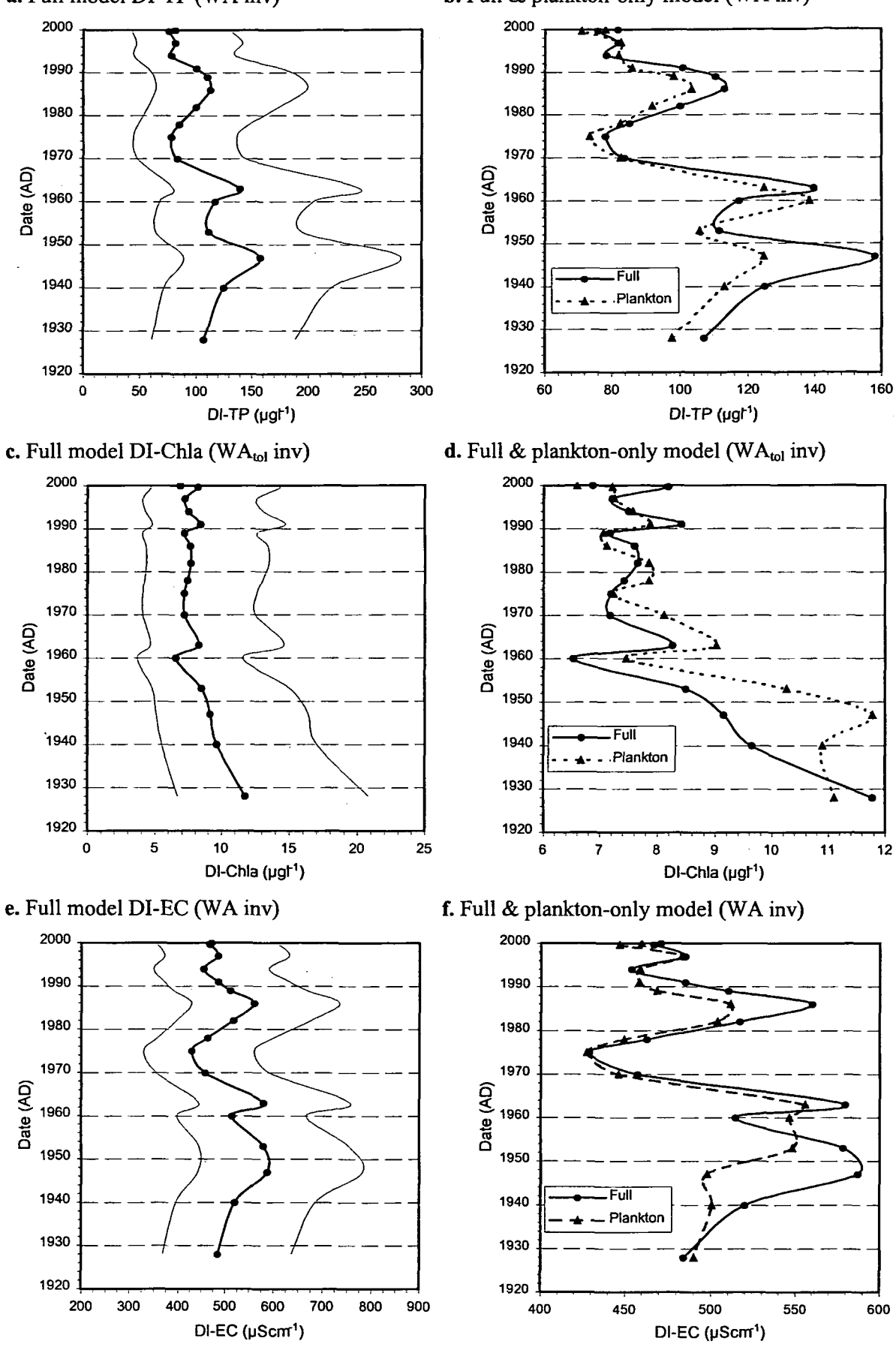


Figure 8.15 **Diatom-inferred TP, Chla and EC reconstructions of DAV00F. On the left are the full dataset model reconstructions (thick line) with standard errors of prediction (thin lines). On the right are comparisons of the reconstructions derived from the full and plankton-only models.**

Diatom-inferred chlorophyll-a reconstruction (DI-Chla)

Figure 8.15c shows the DI-Chla reconstruction for DAV00F according to the WA_{tol} inverse deshrinking model and based on the full dataset. The SEPs (estimated by bootstrapping) again show an acceptable margin of error.

Daventry's DI-Chla reconstruction shows the general trend of decreasing DI-Chla concentrations and thus an improvement in trophic state. Three phases are apparent from the DI-Chla reconstruction. The first is a significant decrease in DI-Chla from 11.8 μgl^{-1} at the core base (1931) to 6.5 μgl^{-1} by 1960. This decrease takes Daventry's DI-Chla concentrations from well within the 'eutrophic' OECD (1982) category, into the 'mesotrophic' category.

The second phase shows a conspicuous increase in DI-Chla between 1960 and 1963, from 6.5 μgl^{-1} to 8.5 μgl^{-1}, taking the reservoir back into the 'eutrophic' OECD category. This increase is only detected in one sample, after which the reservoir's DI-TP returns to the 'mesotrophic' category, dropping back to 7.2 μgl^{-1} in 1970.

The final phase is one of stability, with DI-Chla remaining relatively stable from 1970 to 2000, fluctuating between 6.9 μgl^{-1} and 8.4 μgl^{-1}. This period shows that according to DI-Chla the reservoir has moved from being significantly 'eutrophic' into a relatively stable period just within the 'mesotrophic' classification, with only two samples between 1970 and 2000 breaching the threshold of 8 μgl^{-1} for 'eutrophic' OECD classification.

As for DI-TP, the plankton-only model shows a similar overall pattern to the full model, but with a somewhat different trend in the earliest core section (Figure 8.15d). Instead of a relatively linear decrease in DI-Chla between 1931 and 1960, the plankton-only model shows an initially stable period between 1931 and 1947, after which there is a more rapid decrease to rejoin the trend of the full model reconstruction by 1960.

Diatom-inferred conductivity reconstruction (DI-EC)

Figure 8.15e shows the DI-EC reconstruction for DAV00F, according to the WA inverse deshrinking model and based on the full dataset. The SEPs estimated by bootstrapping once again show an acceptable margin of error.

Daventry's reconstructed DI-EC history follows a similar pattern to its DI-TP trajectory, showing an overall decreasing trend in DI-EC from the core base (1931) to the present day.

As with DI-TP, and unlike DI-Chla, clear stages are not highly apparent. However the overall trend is clear and general phases are discernable.

The first phase is one of high but fluctuating DI-EC (484-587 μScm^{-1}) between 1931 and 1963. The base of the core has a DI-EC of 484 μScm^{-1}, which rises to a peak of 587μScm^{-1} by 1947 before falling back to 514 μScm^{-1} in 1960. It then rises again to a peak of 580 μScm^{-1} in 1963.

The next phase sees a significant decrease in DI-EC between 580 μScm^{-1} in 1963 and 429 μScm^{-1}in 1975. The third phase shows an increase in DI-EC levels from 429 μScm^{-1} in 1975 to a peak of 560 μScm^{-1} in 1986.

The final phase shows a further reduction of DI-EC from 560 μScm^{-1} in 1986 to a low of 454 μScm^{-1} in 1994 followed by a period of relative stability, with DI-EC fluctuating between 454 μScm^{-1} and 484 μScm^{-1} between 1994 and 2000.

The plankton-only model DI-EC reconstruction (Figure 8.15f) follows a similar pattern, showing comparable values to those derived from the full model. However, as with DI-TP and DI-Chla, there is a different trend for the earliest phase in Daventry's history (1931 to 1963). The plankton-only model shows DI-EC fluctuating far less than the full model during this period. Instead, it shows an initially stable period between 1931 and 1947, after which there is an increase in DI-EC to meet the second fluctuating peak shown by the full model in 1963. From 1963 onwards, the reconstructions of the two models converge.

8.4.5 Discussion of Daventry's history

The following palaeolimnological history of Daventry reservoir described in this section is reconstructed from its sedimentary diatom stratigraphy. Furthermore, radiometric dating enables inferences to be made with respect to the timing of important events recorded in the palaeolimnological sequence. However, establishing or pin-pointing the 'exact' causes of events can sometimes prove difficult due to the problem of equifinality, whereby different processes (e.g. land-use change, industrial change, engineering works) can produce the same end result (e.g. changes in water quality).

Diatom data from core DAV00F extend back in time to 1931(±10). Generally the diatom data and diatom-inferred reconstructions show that Daventry's history has been one of

background eutrophy, with periods of hypertrophy, most likely originating from anthropogenic inputs.

The DI-TP reconstructions suggest that eutrophic conditions prevailed between 1931(±10) and 1944(±9). This is highlighted by the presence of *C. radiosa*, a planktonic centric diatom associated with lower nutrient (mesotrophic) conditions. Although DI-TP concentrations imply overall eutrophy during this period, the DI-Chla reconstructed values indicate hypertrophy. High DI-Chla levels at this time may be attributed in part to the high concentrations of *Pediastrum boryanum* microfossils (Eastwood *et al.*, 2002, unpublished), perhaps indicating that during this period, greater competition from green algae existed. Reynolds (1984b) classifies *P. boryanum* as a hypertrophic early-summer species that replaces spring blooms of *Stephanodiscus* spp. in hypertrophic systems. The high levels of green algal microfossils, favouring hypertrophic conditions, which are present at this time, may bring into question the eutrophic DI-TP classification assigned to this phase.

Between 1944(±9) and 1967(±8) high DI-TP and DI-EC values are observed. *Stephanodiscus hantzschii*, *S. hantzschii* fo. *tenuis* and *S. parvus* are planktonic centric diatoms associated with nutrient-rich waters (cf. Anderson, 1990; Bennion, 1995). *C. dubius* and *C.* cf. *tholiformis* are also indicative of eutrophic-hypertrophic waters; these diatom taxa are collectively present throughout the diatom sequence in DAV00F. These diatom taxa experience variations in relative abundance that may be due to competitive interactions brought about by fluctuations in environmental conditions that favour different taxa in different years. *C. meneghiniana* reaches a peak at 29.5 cm (1960±9) and is also considered to be indicative of highly eutrophic conditions and is capable of withstanding high ionic concentrations (Kolbe 1932; Round, 1998; Håkansson & Korhola, 1998). The presence of *C. meneghiniana*, together with high relative abundances of *Stephanodiscus hantzschii*, *S. hantzschii* fo. *tenuis* and *S. parvus* between 1944(±9) and 1967(±8) indicate a period of hypertrophy, coinciding with a decline in the relative abundance of *C. dubius* and elimination of *C. radiosa*. The causal mechanism for these changes may have been pollution arising from the Victorian sewage works, or perhaps stemming from the post-war intensification of agriculture in the reservoir catchment. Further evidence to implicate failings in the sewage works is provided by the marked increase in concentrations of heavy metals in this section of the core (Eastwood *et al.*, 2002, unpublished). Contamination of the reservoir water by heavy metals implies direct pollution from the treatment works during this period and highlights the inadequacies of a 'low-tech' treatment process that probably continued to release heavy metals, and presumably nutrients, into the reservoir.

Decade	Historical or Known Events	Palaeolimnological Events
1800s	Reservoir constructed (1804) Sewage works built (1890s)	
1910s	1914-1939: Reservoir dredged sometime between the two world wars.	Prior to 1944 ±9 yrs: Eutrophic conditions prevail at the site.
1920s		
1930s	1930s-1960s: Metal processing carried out in catchment (including Ni, Zn, Cu and Cr). Chromium and arsenic found in sludge lagoons connected with sewage works.	
1940s	Late 1940s-1960s: Intensification of agriculture in catchment	
1950s		1944-1967: Hypertrophic conditions.
1960s	1965-1975: Daventry town expands rapidly both in area and population	
1970s	1969-70: Spillway constructed and reservoir water level reduced by 90%. 1970s: Pollution incident – release of several thousand gallons of heating oil from the Fords' plant. 1972-3: Grit trap constructed during winter/spring (emptied twice during the period 1973 to 1997) 1974: Sewage works decommissioned	1967 ±8 yrs: Reservoir commences a period of recovery.
1990s	1992: Sewage works site reclaimed (waste from sludge lagoons placed in clay-lined pits and reed bed planted) 1997: Grit trap dredged/emptied	1993 ±4 yrs: Marked improvement and stabilisation in trophic status (eutrophic conditions)
2000		2000: Sediment cores taken

Table 8.10 Outline of historical and palaeolimnological events at Daventry Reservoir.

Eutrophic and hypertrophic conditions prevailed at the site until 1967(±8) when the commencement of a period of recovery from nutrient enrichment is observed in the DI-TP, DI-EC, DI-Chla and *P. boryanum* concentrations. This is also evidenced by the reappearance and subsequent increase in *C. radiosa* towards the core top. *C. radiosa* is reported to be widely distributed in oligotrophic to mesotrophic lakes throughout the world (Huber-Pestalozzi, 1942) and is thus considered most competitive in P-limited environments. For example Lotter *et al.* (1998) found *C. radiosa* to be most abundant in Alpine lakes classified as mesotrophic according to OECD (1982) criteria, although it was also present at lower percentage relative abundance in eutrophic sites. In Marsworth Reservoir, southeast England, Bennion (1994) presented palaeolimnological evidence illustrating a decrease in *C. radiosa* since the 1970s, subsequent to an increase in sewage effluent discharge into the reservoir. Stoermer *et al.* (1987) reported that *C. radiosa* (termed *C. comta*) is extremely rare in modern samples from Lake Ontario, but was an important element of the phytoplankton prior to eutrophication. In the UK lowland reservoirs

calibration set, a TP optimum of 48 μgl^{-1} is derived for *C. radiosa*, its presence is recorded in reservoirs with TP concentrations up to ~100 μgl^{-1}, but never as a dominant species.

The period of recovery from nutrient-enrichment (hypertrophic to eutrophic conditions) beginning in ~1967(±8), may have been initiated by up to three historical events. Firstly, the grit trap was constructed in the winter-spring of 1972-3; secondly, the Victorian sewage works constructed at the southern edge of the reservoir during the 1890s was decommissioned in 1974; and thirdly, the sustained period of Daventry town's expansion between 1965 and 1975, which converted 70% of the catchment from agricultural land-use to urban development. These three changes are in close chronologically proximity to one another and each event may have acted separately or in tandem to bring about a change in the nutrient status of the reservoir. Moreover, it is possible that other unknown causal mechanism(s) may have been responsible for the changes in nutrient concentrations observed in the palaeoenvironmental record. A higher resolution study of the diatom flora and data on the turnover time of the reservoir around this time period may provide further information that may aid delineation of the relative importance of these events in respect of lake recovery. However it is doubtful whether chronological separation of these causal mechanisms is feasible, since the dates ascribed to the core have relatively high associated error margins that cannot be overcome by pursuing a higher resolution study.

The improved nutrient status of the reservoir from 1967(±8) is sustained and, aside from *C. radiosa*, the planktonic pennate diatom *F. crotonensis* occurs in low abundance towards the top of the core. This taxon is commonly associated with relatively clear meso-eutrophic waters (Reynolds *et al.*, 1983). The planktonic pennate diatom *A. formosa* continues to occur towards the top of DAV00F. This taxon is similar to *F. crotonensis* since it is also found in meso-eutrophic waters blooming in clear waters rich in nutrients (Lund, 1950; Reynolds & Irish, 2000). Importantly, these taxa do not compete so well for nutrients against the medium sized centric diatoms, e.g. *C. dubius* and *C. radiosa*, which tend to bloom later in the year or at times when Si concentrations and/or light intensity are less favourable for *F. crotonensis* and *A. formosa* (Tilman *et al.*, 1982; Bradshaw & Anderson, 2002).

A further increase in *C. radiosa* dated to 1993(±4) in core DAV00F suggests a marked improvement in the trophic status of the reservoir. DI-TP is at its lowest level and remains remarkably stable during this most recent period. Currently, Daventry reservoir has an annual average TP of 84 μgl^{-1} (Table 4.3), although concentrations are highly variable

throughout the year (range 24-189 μgl^{-1} (measured in this study)). This phase begins very shortly after, and appears to coincide with, the 1992 engineering works that finally reclaimed the site of the sewage works. The engineering works were multi-faceted in nature and entailed excavation of the sludge lagoons and burial of the waste into clay-lined pits. The spring, which also fed the sewage works, presently flows through the area of the old sludge lagoons, which is now a reed bed (*Phragmites australis*). If improvements in Daventry's trophic state at this time are attributable to the engineering works and not to some other unknown causal mechanism(s), this would suggests that the turnover time of the reservoir is relatively rapid. This in turn suggests that the driving force behind the improvement in nutrient status from 1967(±8) was the reservoir ceasing to receive sewage from Daventry town.

The diatom data thus appear to be in broad agreement with historical data, indicating hypertrophic conditions prior to 1967(±8) and subsequent recovery to eutrophy when the reservoir ceased to receive sewage from Daventry town in 1974. Further improvement and stabilisation of water quality since 1993(±4), appears to coincide with the extensive engineering works of 1992 that finally reclaimed the site of the sewage works. The present-day diatom assemblage in Daventry reservoir may indicate either full recovery to a new equilibrium or a phase in the recovery process. Populations of *C. radiosa*, *C. pseudostelligera* and *C. dubius* have returned to pre-perturbation levels, however the post-perturbation presence of *A. granulata* var. *angustissima*, *C. atomus*, *F. crotonensis* and *A. formosa* suggest that Daventry reservoir's current diatom assemblage may be undergoing progress towards a new equilibrium. Since post-perturbation responses of diatoms have not been so widely monitored and tend to follow stochastic changes, it is not yet known whether the current diatom assemblage has reached equilibrium (cf. Anderson *et al.* 1990). It is difficult to be sure whether the species composition of the current diatom assemblage will remain stable, will progress to a new equilibrium, or whether there will be a complete reversal to the pre-perturbation floristic composition. Future monitoring of Daventry reservoir's diatom species dynamics should expose the full extent of post-perturbation recovery trends.

8.5 Discussion

8.5.1 Reliability of environmental reconstructions

Confidence in reconstructed values was assessed by the simple method of calculating the proportion of species data in each fossil sample consisting of taxa that are either 'rare' or

absent in the calibration set (Birks, 1998). The optima of rare taxa may be poorly modelled, therefore if rare taxa are present in high abundance in fossil samples, this may lead to inaccurate environmental reconstructions. To enable an assessment of the extent of this problem in the current study, a cut-off of occurrence in 10% of sites (i.e. species present in >4.2 sites) was used to determine rare taxa.

BBK00C		DAV00F	
Depth (cm)	% taxa rare/absent (full model)	Depth (cm)	% taxa rare/absent (full model)
AullsIan 0.75	6.9	0.25	3.58
ThalPseu/ 1.25	9.2	1.25	2.07
AullsIan 1.75	10.6	3.25	2.94
2.25	6.2	5.25	4.57
2.75	19.7	7.25	4.43
3.25	13.3	9.25	0.64
3.75	17.9	11.25	3.16
4.25	35.1	13.25	6.09
AullsIan 4.75	35.9	15.5	3.40
5.75	40.2	18.5	2.98
6.75	44.0	21.5	2.75
7.75	21.1	NavTrv 25.5	5.78
8.75	20.2	NitzCap/NavRhyn 29.5	10.80
9.75	13.8	AmpVen/TryLev	
12.50	4.7	33.5	2.34
15.50	1.4	37.5	4.36
18.50	0.9	41.5	3.50
21.50	1.9	45.5	0.32
24.50	0.8		
27.50	2.8		
30.50	0.5		
33.50	1.4		
36.50	2.8		
39.50	2.3		
SynNana 42.50	5.0		

Table 8.11 Percentage of taxa either rare or absent in the UK lowland reservoirs calibration set, that occur in cores BBK00C and DAV00F. Shaded areas show core sections where the named taxa predominate the percentage of rare / absent taxa (see text for details).

Approximately 64% (58 out of 90) of the diatom taxa identified in BBK00C are present in the modern calibration set. The majority of taxa missing from the calibration set occur only at low percentage relative abundances. Two taxa present in Blackbrook's fossil record at relatively low values but displaying a reasonably well defined stratigraphy and are absent from the modern calibration set, are *T. pseudonana* towards the core top (12 samples, 5% max) and *Synedra nana* at the core base (2 samples, 2% max), both of which are largely planktonic species. One of the dominant planktonic taxa in the upper sediments of the core, *A. islandica* occurs in the calibration set but is only present in 4 sites (<10%), of which Blackbrook is one. This taxon is described as 'rare/absent' in the UK lowland reservoirs calibration set. Consequently, the optimum derived for *A. islandica* may be subject to error and in turn, DI-TP estimates derived from samples where *A. islandica* occurs at high relative abundance (e.g. ~2.5-10.5 cm in BBK00C), should be interpreted with caution.

In DAV00F, approximately 61% (54 out of 88) of diatom taxa identified in the fossil record are also present in the modern calibration set; a slightly lower, but comparable figure to that recorded in BBK00C. Few of these taxa are classified either as rare in the core sequence, or present in the fossil record but absent from the UK lowland reservoirs calibration set. Of the taxa present in the fossil record but absent from the calibration set, the majority occur in only a small number of samples, and where they do occur, it is at low relative abundance. The highest maximum percentage relative abundance for an individual taxon occurring in DAV00F but absent from the calibration set is 3.6% for *Navicula trivialis*. The 29.5 cm sample from DAV00F contains the highest percentage of rare / absent taxa (10.8%), predominantly comprising periphytic taxa, the most significant of which are *Nitzschia capitellata*, *Navicula rhyncocephala*, *Amphora veneta* and *Tryblionella levidensis*.

The data for both Blackbrook and Daventry indicate that the majority of samples do not have problems associated with a lack of 'modern analogues', and therefore the diatom-inferred environmental reconstructions should be reliable. However, as discussed above, questionable reconstruction results may arise from the ~2.5-10.0 cm section of the core BBK00C, where *A. islandica* is the dominant diatom taxon (see section 8.5.3).

8.5.2 Species trends in the fossil diatom records of BBK00C and DAV00F

A DCA ordination was performed to investigate the change over time in fossil diatom assemblage composition at Blackbrook and Daventry reservoirs, and to examine these trajectories in relation to the calibration set species data. This facilitates assessment of the degree to which the calibration set species data encompass the fossil diatom data, which in turn allows evaluation of the robustness of environmental reconstructions. The modern surface sediment diatom species assemblage from the UK lowland reservoirs calibration set were active in the DCA, with the fossil samples from cores BBK00C and DAV00F included as passive (Figure 8.16). Samples from the two cores are plotted in order of stratigraphic sequence, with adjacent samples connected by lines. Arrows on the time trajectory lines indicate the direction from core top to core bottom (i.e. young to old).

The trajectories illustrated for both BBK00C and DAV00F indicate that there is no overlap in the species assemblages between these two sites. This supports the earlier decision to select the two sites on account of their differing assemblages, thus enabling the UK lowland reservoirs inference models to be tested across as broad a range of diatom species assemblages as possible. Figure 8.16 also illustrates that the down-core diatom assemblages of both Daventry and Blackbrook reservoirs lie within the range of modern diatom

assemblages incorporated in the calibration set, thus further supporting the inferences made in section 8.5.1.

The time trajectory for Daventry reservoir indicates an overall cyclical pattern, with the surface sediment sample comprising a similar assemblage to samples seen at the base of the core. This supports the discussion in section 8.4.5 that the reservoir has changed from eutrophic to hypertrophic and back to eutrophic and the associated species assemblages have shifted correspondingly. Although the assemblage is now similar to that seen at the base of the core, it is not (yet) identical, but may instead be in the process of attaining a new equilibrium comprising at least some components of the former eutrophic assemblage. The 33.5 cm sample consists of a large proportion of *S. parvus*, making this sample the most distinct in the core, and most similar in composition to samples seen during Blackbrook's initial phase of development. The calibration set sites that have diatom assemblages most similar to those recorded throughout DAV00F (not including Daventry itself), are Weir Wood (site 45), Nanpantan (site 21) and Stanford (site 27). These sites have surface sediment diatom assemblages dominated by *C. radiosa*, *C. dubius*, *A. granulata* var. *angustissima* or *S. parvus*, with other species including *C. invisitatus*, *C.* cf. *tholiformis*, *Stephanodiscus hantzschii* fo. *tenuis* and *A. formosa*.

Blackbrook's time trajectory indicates that its surface sediment sample is the most different and distinct from the other samples in the core. This has been interpreted as a seasonal artefact, representing the dominant taxa blooming in the period immediately prior to sediment sampling (section 8.3.5). The taxa seen in Blackbrook's surface sediments are most similar to those in Ardleigh (site 1) and Blithfield (site 4), including species such as *A. normanii* fo. *subsalsa* and *Stephanodiscus neoastraea*; although these sites also differ in their assemblages in some respects (e.g. they do not contain *A. islandica*). The samples towards the top of BBK00C that are dominated by *A. islandica*, are most similar to the calibration set assemblages of Swithland (site 31) and Thornton (site 32). The section of core BBK00C containing the highest proportions of *A. subarctica*, *A. formosa*, *F. crotonensis* and/or *A. ambigua* are most similar to Wistlandpound (site 38) and Clatworthy (site 8). The earliest history of Blackbrook sees a diatom assemblage most similar to that found in Hawkridge (site 17), and relatively similar to those of Tittesworth (site 33) and Ogston (site 22). These sites have assemblages dominated by *A. formosa*, with *C. radiosa* and/or *S. parvus* as sub-dominants.

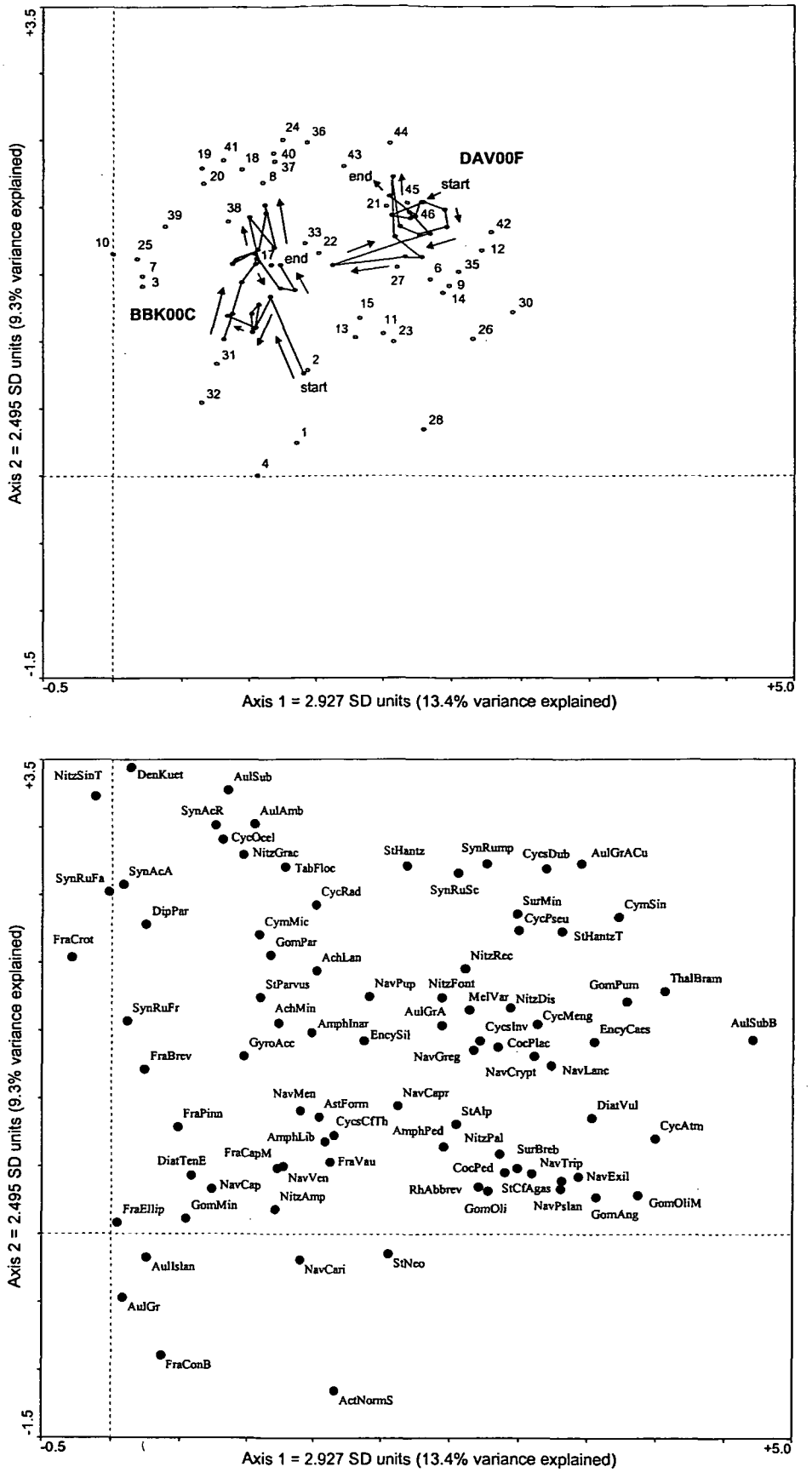


Figure 8.16 a&b **(a) shows a surface sediment diatom species DCA ordination with fossil samples from cores BBK00C and DAV00F plotted as passive. Fossil samples are plotted from youngest to oldest stratigraphic depth. Adjacent samples are joined to show a time trend (direction of increasing core depth indicated by arrows). Surface sediment species are plotted separately in (b).**

8.5.3 Evaluation of the reconstruction capabilities of the UK lowland reservoir and EDDI Combined DI-TP models in BBK00C and DAV00F

To assess the reconstruction capabilities of the UK lowland reservoirs DI-TP inference model, reconstructions were performed on the fossil diatom assemblages in cores BBK00C and DAV00F using both the UK lowland reservoirs WA_{tol} classical deshrinking model (based on the full species dataset) and the EDDI Combined TP LWWA model.

Core BBK00C

In the EDDI Combined TP calibration set *A. islandica* is better represented than in the UK lowland reservoir calibration set, occurring in 41 out of 347 sites (~12%) at a maximum percentage relative abundance of 22.1%. The TP optima assigned to *A. islandica* in the UK lowland reservoirs DI-TP calibration set is high at 102 μgl^{-1} TP, but in the EDDI Combined TP calibration set its optimum is considerably lower at 33 μgl^{-1}. Optima derived from the NW European (Bennion *et al.*, 1996) and Swedish (Bradshaw & Anderson, 2001) calibration sets are 70 μgl^{-1} and 44 μgl^{-1} respectively, further supporting the suggestion that the optimum derived for *A. islandica* in this study is probably overestimated and thus reconstructed TP values in samples where *A. islandica* is dominant are most likely also overestimated.

The DI-TP trajectories calculated using both the UK lowland reservoirs full model and the EDDI Combined TP model are plotted alongside one another in Figure 8.17. For Blackbrook, both models show similar trends of low, stable TP concentrations (30-50 μgl^{-1}) from 42.5-15.0 cm. Consistently lower inferred values derived from the UK lowland reservoirs model occur throughout this section, despite the slightly higher optima of the dominant taxa e.g. *S. parvus*, *A. formosa*, *F. crotonensis* and *A. subarctica* in the UK lowland reservoirs model. The lower reconstructed values for the UK lowland reservoirs model may reflect differences in the statistical foundation of the models applied - LWWA for the EDDI Combined TP model as opposed to WA_{tol} classical for the UK lowland reservoirs model. The high tolerances of the aforementioned dominant taxa leads to their downweighting during construction of the WA_{tol} classical model and may subsequently result in lower reconstructed TP concentrations than those derived from the LWWA model.

Between 15.0 and 4.0 cm, the UK lowland reservoirs full model shows rapidly increasing DI-TP concentrations, whereas the EDDI Combined model continues to indicate relatively stable values throughout this period where *A. islandica* dominates the record (subzone B-

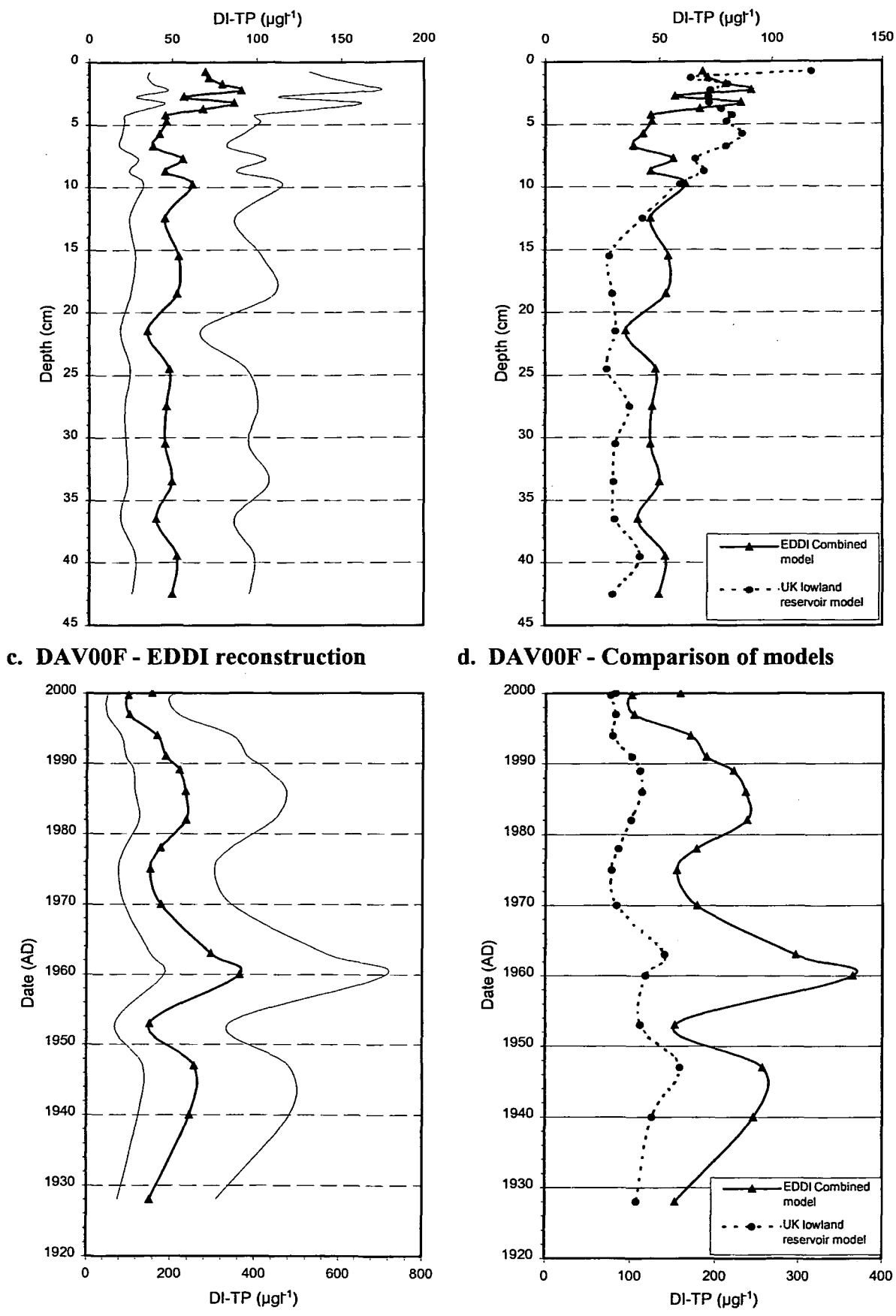


Figure 8.17 **Comparisons of DI-TP reconstructions for BBK00C (a & b) and DAV00F (c & d) cores using the EDDI Combined TP LWWA model and the UK lowland reservoir full WA_{tol} classical deshrinking model (a & c show EDDI reconstruction with associated prediction errors; b & d show comparison of EDDI and UK lowland reservoir reconstructions).**

4b). From 4.0-1.0 cm (subzone B-5a), the reconstructed TP values of the two models reconverge, although the UK lowland reservoirs model reconstructs more stable TP values than those derived from the EDDI Combined TP model. Thus the UK lowland reservoirs model may predict more stable TP concentrations in this zone since some of the species occurring in this subzone are underrepresented or aggregated in the EDDI Combined TP calibration set. These species include; *A. normanii* fo. *subsalsa*, which is not included in the EDDI Combined TP model; *A. granulata*, which is of common occurrence in the calibration set (124 sites), but is an aggregated taxon (inclusive of *A. granulata* var. *angustissima*) and thus may have been assigned a compromised TP optimum; *T. pseudonana*, which only occurs in 1 site at 1% relative abundance, indicating that its optimum (144 μgl^{-1}) is probably poorly predicted. *T. pseudonana* does not occur in the UK lowland reservoirs calibration set, therefore when the UK lowland reservoirs model is applied, *T. pseudonana*'s occurrence in fossil samples cannot adversely affect inferred values.

The reconstructed TP values for the surface sediment sample differ markedly between the two models. The EDDI Combined TP model infers values of ~60 μgl^{-1}, whereas the UK lowland reservoirs model implies values >100 μgl^{-1}, compared with a current measured annual mean TP concentration of 118 μgl^{-1}. The distinct differences between the two reconstructed values probably arise because *S. neoastraea* is a sub-dominant in this sample and its optimum is assigned as only 68 μgl^{-1} in the EDDI Combined TP model, but ~25% higher (93 μgl^{-1}) in the UK lowland reservoir model. In addition, as discussed above, *A. normanii* fo. *subsalsa* is not assigned an optimum in the EDDI Combined TP model; however the optimum assigned to this taxon in the UK lowland reservoirs model is high at 130 μgl^{-1}, partially determining the high inferred value for the surface sediment sample. The lower inferred TP concentration under the EDDI Combined model for the surface sediment sample is probably most influenced by the high proportion of *A. formosa*. This taxon has similar optima in both calibration sets (48 μgl^{-1} and 44 μgl^{-1} for the EDDI and UK reservoirs models respectively), but the dominant influence of this taxon is not regulated in the EDDI Combined TP model by the high optima taxa *S. neoastraea* and *A. normanii* fo. *subsalsa*.

Core DAV00F

The EDDI Combined model DI-TP reconstruction shows a similar overall trend to that derived from the UK lowland reservoirs model. However, the EDDI Combined TP model DI-TP reconstruction trajectory predicts significantly higher absolute values. This amplification is most prominent during periods when *C. meneghiniana* and *Stephanodiscus* spp. e.g. *Stephanodiscus hantzschii* and *S. hantzschii* fo. *tenuis* dominate the diatom

assemblage of DAV00F. The UK lowland reservoirs model implies a present-day TP concentration of 82 μgl^{-1}, whereas the EDDI Combined TP model predicts a modern TP concentration of approximately double this value (158 μgl^{-1}). The contemporary mean annual TP concentration measured in the current study was 84 μgl^{-1}. The UK lowland reservoirs model therefore appears to most accurately predict current TP concentrations.

The optima for *Stephanodiscus hantzschii* and *C. meneghiniana* may be better defined in the EDDI Combined TP calibration set. Although *Stephanodiscus hantzschii* is an 'aggregated' taxon in this model (i.e. there is no separate optima for *S. hantzschii* fo. *tenuis* since it is aggregated with *Stephanodiscus hantzschii*), its optima is derived from data based on percentage relative abundances (36% max) from 148 sites. *C. meneghiniana* occurs in 90 sites and at 30% maximum values. The optima derived for these taxa in the EDDI Combined TP calibration set are 190 μgl^{-1} TP and 254 μgl^{-1} TP respectively. These optima are considerably higher than those derived in this study (71 μgl^{-1} (103 μgl^{-1} for *S. hantzschii* fo. *tenuis*) TP and 115 μgl^{-1} TP respectively). Although these optima are amongst the highest of all TP optima derived in this study, they are only approximately half those used for reconstructions in the EDDI Combined TP calibration set.

The optima for both *C. meneghiniana* and *S. hantzschii* fo. *tenuis* are probably underpredicted in the current study because abundance curves for these taxa (Figure 7.5a) clearly indicate a sigmoidally increasing curve that is truncated at the high end, denoting that these taxa have not been sampled across their full tolerance range. It is not known whether the optima of *Stephanodiscus hantzschii* has been underestimated in the current study because this taxon appears to show little response to TP (Figure 7.5a) since it is found in sites spanning a broad range of TP concentrations. Hence the aggregated taxon *Stephanodiscus hantzschii* in the EDDI Combined TP model may be overpredicting the optima of *Stephanodiscus hantzschii* in the process of aggregating all the forms of *Stephanodiscus hantzschii* into one 'taxon'. Consequentially the optima of *Stephanodiscus hantzschii* may better reflect the optima of the form *S. hantzschii* fo. *tenuis* than of the nominate *Stephanodiscus hantzschii*.

8.5.4 Comparative performance of the diatom-inferred total phosphorus (DI-TP), chlorophyll-*a* (DI-Chla) and conductivity (DI-EC) models in BBK00C and DAV00F

Comparison of full vs. plankton-only model reconstructions

In both Blackbrook and Daventry reservoirs, the UK lowland reservoirs full and plankton-only models infer similar TP, Chla and EC values. Where there are differences between the values reconstructed using the full and plankton-only models, this appears to be the result of either inconsistencies in the WA optima derived using the different models, or because the inclusion / exclusion of periphytic taxa affects the inferred values. This supports the observations of Bradshaw *et al.* (2002), that when sediment records are dominated by planktonic diatom taxa, reconstructed values will be very similar regardless of whether a plankton-only or full model is utilised.

Although in general, species optima vary little between the two datasets, there are some inconsistencies e.g. *D. tenuis* var. *elongatum* has a TP optima 10 μgl^{-1} lower in the plankton-only model. However, the differences are generally small and unlikely to fully explain the observed differences in overall reconstruction trends.

The most plausible explanation for the variation in reconstructed values between the two models is the inclusion of periphytic taxa in the full model. In Daventry, between 1930 and 1960, the reconstructed values are consistently higher under the full model for both DI-TP and DI-EC, whereas they are lower for DI-Chla. This discrepancy arises because the periphytic taxa included in the full model generally have more extreme TP, Chla and EC optima. For example, *N. amphibia* has both high TP and EC optima and frequently occurs in this core section (maximum 5% relative abundance), thus increasing the DI-TP and DI-EC values reconstructed over this period. In respect of periphytic taxa exhibiting low Chla optima, no single taxon drives the lower DI-Chla values reconstructed under the full model. Instead it is the combined influence of numerous periphytic taxa during this period, which have low Chla optima (Figure 7.7) and also show a poor relationship to Chla (Figure 7.8a). For example, *Cocconeis placentula*, *Rhoicosphenia abbreviata*, *Gomphonema parvulum*, *Gomphonema olivaceum*, *A. minutissima* and *Navicula lanceolata* occur at low relative adundance but exhibit low Chla optima, and appear to have the combined effect of lowering DI-Chla under the full model.

The reconstruction for Blackbrook reservoir is similar whether the full or plankton-only model is employed. However in Daventry reservoir, as discussed above, there are

discrepancies between the reconstructed values derived from the different models. The plankton-only DI-Chla reconstruction may offer an improvement over the full model at this site. Periphytic taxa show little or no relationship to Chla and exhibit extreme Chla optima, thus they appear to prematurely lower DI-Chla values. The plankton-only model maintains a high DI-Chla until 1950, corresponding to the trend seen in the chlorophyte stratigraphic profile (*P. boryanum* specifically).

Taxon-environment relationships

Although the lowland reservoir calibration dataset appears to cover the range of chemical conditions experienced over time by both Blackbrook and Daventry reservoirs, it may not describe accurately the distribution of individual diatom taxa along the ecological gradients of interest. Species distributions may be truncated and hence a taxon's optimum poorly predicted. Graphical representations of species distributions are seen in Figures 7.5a/b (TP), 7.8a/b (Chla) and 7.11a/b (EC). Examination of these dataset characteristics improves our understanding of the underlying species distribution patterns, enabling a more objective evaluation of model performance. Reconstructed values for fossil samples consisting of taxa with poorly modelled optima (i.e. truncated distribution graphs), or dominated by taxa showing no clear relationship to the environmental variable under reconstruction, should be treated with caution. The accurate definition of species' optima is considered in more detail in Chapter 9.

Environmental optima derived from the WA models for individual taxa are not ecologically exact and are therefore "not strictly of ecological relevance" (Bradshaw *et al.*, 2002, p.1970). This is because optima more intimately reflect the statistical methods used to derive the values than the seasonality of individual diatom species and the ambient environmental conditions at the time of growth. However this problem is partially overcome through the utilisation of mean annual water chemistry data, that is intimately linked with accompanying 'annual average' surface sediment diatom assemblages. The strong seasonality of many diatom taxa means that it is important that the measured contemporary water chemistry reflects the full range of seasonal variability (Bennion & Smith, 2000).

WA optima derived from surface sediment diatom assemblages and contemporary water chemistry are based on relative species abundances and not on diatom biovolumes. The reconstructions based on these WA optima use percentage relative abundance data and thus take no account of the overall productivity of a system. This is problematic particularly when reconstructing trophic status, since very productive systems are treated as equivalent

to unproductive systems, in that only variations in species dynamics are incorporated into the models applied. Also, diatoms are only one of a number of different algal groups. Reconstructed values take no account of the presence of other algal groups and their (competitive) interactions throughout the year. Other algal groups impact upon the available nutrient resources and measured epilimnetic TP concentrations will also include the nutrients locked up in individuals from these other algal groups. Therefore, reconstruction of only one environmental variable may not accurately reflect the overall phytoplankton dynamics of a waterbody.

Since TP and Chla represent different axes in the CCA ordination diagram (Figure 5.6), they would be expected to reflect different aspects of a site's environmental history. This is exemplified in Daventry reservoir, where this site's DI-Chla reconstruction shows a differing trend to DI-TP in zones D-1 and D-2, with DI-Chla increasing and DI-TP decreasing. Without further information on site history, this would appear to be an anomaly, because both high TP and high Chla concentrations are considered indicators of eutrophic conditions. However examination of other microfossil stratigraphies at Daventry shows that concentrations of *Pediastrum boryanum* were also very high in zones D-1 and D-2. Large *P. boryanum* populations may have stripped the water of available P and locked it into their biomass. Consequently, although the water may have been eutrophic, the P available to algal groups other than *P. boryanum*, may not have been so high through much of the season, favouring diatom taxa with lower P optima. This may have masked the actual TP concentration of the reservoir in the diatom-inferred reconstruction. Only through application of both DI-Chla and DI-TP reconstructions can a better understanding of phytoplankton interactions be achieved. The majority of published studies where inference models are applied only tend to apply one or the other, DI-TP or DI-Chla models. However diatom-based reconstructions from Daventry reservoir have shown that the creation and application of both DI-TP and DI-Chla models, and their interpretation in the light of additional environmental proxies may avoid the possible masking effects of competition from phytoplankton groups beyond the diatom community and in turn aid the interpretation of a reservoir's trophic history. This adds support to the value of applying multi-proxy reconstructions, particularly when inference models are based on calibration sets with two clear axes of variation (e.g. UK lowland reservoirs) and where the sites at which environmental variables are reconstructed appear to show more than one main axis of variation (e.g. Daventry reservoir).

The UK lowland reservoir inference models have the ability to successfully reconstruct TP, Chla and EC trajectories at both Blackbrook and Daventry reservoirs. It has not been possible to test the validity and reliability of these reconstructions through comparison with historic water chemistry data, however the model-derived trends appear to be consistent with historical events recorded at both sites. Since both TP and EC were seen to influence diatom distributions along the same axis of variation (see Chapter 5), it is not surprising that the DI-TP and DI-EC reconstructions also follow similar trends. Thus little extra information is gleaned from reconstructing both TP and EC at either Daventry or Blackbrook. However since Chla influences diatom distributions along a different ordination axis (axis 2 in the ordinations presented in Chapter 5), DI-Chla reconstructions are slightly different to those derived for TP and EC.

8.6 Summary Points

- Taphonomic issues (i.e. diatom dissolution) do not appear to be a problem in the sediment records of either Blackbrook or Daventry reservoir. Hence, it is appropriate to apply quantitative DI-reconstructions at these sites.
- The fossil diatom assemblages throughout cores BBK00C and DAV00F lie within the TP, Chla and EC gradients spanned by the UK lowland reservoirs calibration set. Therefore the environmental reconstructions for cores BBK00C and DAV00F derived from the UK lowland reservoirs inference models are considered to be reliable.
- Application of the UK lowland reservoirs inference models to Blackbrook reservoir appears to reconstruct the reservoir's entire history since construction in 1906. An initial stabilisation phase is followed by a prolonged period of relative stability. Subsequently there has been a change in diatom populations, mirrored by increasing DI-TP, DI-Chla and DI-EC values. The cause of this change may be attributed foremost to an increase in nutrient loadings, but may latterly also relate to the impact of artificial aeration.
- Application of the UK lowland reservoirs inference models to Daventry reservoir (DAV00F) indicates that the reservoir has been eutrophic since the 1930s. There was a period of hypertrophy from the late 1940s to late 1960s. However the reservoir has since returned to an improved trophic state, which is probably attributable to reclamation of the sewage works site adjacent to the reservoir.
- The diatom-inferred reconstructions provide a reasonable estimation of the degree of disruption / recovery of both Blackbrook and Daventry's aquatic ecosystems due to land-use change and anthropogenic impact.

- The inference models are able to reconstruct broad perturbations in water quality. However they appear to be insufficiently sensitive to reconstruct small changes in TP, Chla and EC. This, combined with dating errors, can make event-specific changes in water quality difficult to delineate, especially when they occur over a relatively short period of time.
- DI-Chla reconstructed values for Daventry reservoir indicate that competitive influences of other algal groups aside from diatoms may have masked the hypertrophic status of the reservoir between the 1930s and late 1940s resulting in underestimation of DI-TP during this period.
- The DI-TP and DI-EC reconstructed values for both BBK00C and DAV00F follow similar trends, probably because both TP and EC co-vary along axis 1 of both the PCA and CCA ordinations (see Chapter 5).
- DI-Chla reconstructed values tend to follow an overall similar trend to DI-TP and DI-EC reconstructions, although they appear less correlated in certain sections of the cores. These differences can be explained by fluctuations in other algal groups, and also likely reflect the influence of Chla along axis 2 of both the PCA and CCA ordinations (see Chapter 5).
- The diatom species assemblages present throughout both BBK00C and DAV00F fall within the ordination space defined by the UK lowland reservoirs calibration set. There are few samples where the percentage of rare / absent taxa is >5% and few problems in finding modern analogues.
- Under-representation of *A. islandica* in the UK lowland reservoirs calibration set and probable over-prediction of the TP optimum of this taxon suggests that DI-TP estimates derived from samples with high percentage relative abundances of *A. islandica* should be interpreted with caution.
- The inclusion of lower TP sites to increase the range of TP covered by the calibration set at the low end may improve the WA optima derived for taxa such as *C. radiosa* and *A. islandica*. However it is unlikely that many more low TP UK lowland reservoirs exist and improved optima may only be derived through the amalgamation of datasets e.g. the EDDI Combined TP model. However, taxonomic harmonisation and species amalgamations create their own inherent problems.
- The inclusion of higher TP sites to increase the range of TP covered by the calibration set at the high end may improve the WA optima derived for taxa such as *Stephanodiscus hantzschii* and *C. dubius*. However, as shown in Figures 9.3 and 9.4, it may not be worth including higher TP sites because there appears to be little change in diatom species assemblages above approximately 150 gl^{-1} TP. Multi-

proxy studies may provide more useful ecological information above this TP concentration.

- Physical factors and reservoir management practices e.g. the use of artificial destratification techniques can be just as important in explaining shifts in taxon relative abundances as chemical parameters. Hence it is important to have access to dated sediment core sequences and sufficient historical evidence to enable critical analysis of inference model reconstruction capabilities.
- There is an argument for performing environmental reconstructions for more than one variable, particularly if the calibration set used to perform the reconstruction shows more than one strong axis of variation and thus should enable a more comprehensive interpretation and evaluation of observed species shifts.

PART FOUR

Discussion & Conclusions

CHAPTER NINE

Reservoir eutrophication: an assessment

9.1 Introduction

This chapter expands upon earlier discussions to examine broader themes. It focuses on a number of inter-related issues, associated both with the methodologies employed in, and the results generated by this study. The topics fall under the broad themes of i) inference model development and ii) axes of variability in the environmental and species data. Both topics are set within the overarching framework of eutrophication assessment in UK lowland reservoirs.

9.2 Creation and application of inference models

With specific reference to UK lowland reservoirs, Figure 9.1 illustrates the various phases in the development and application of inference models. At each stage of the process it was necessary to make decisions – many subjective – that directly impacted upon subsequent stages and in turn influenced the overall outcome of the inference model approach. Many of these issues have been discussed elsewhere in this thesis; therefore this section expands upon key issues relating to the use of diatom-based inference models in the assessment of eutrophication in UK lowland reservoirs. Topics discussed include i) the reconstruction of a single environmental gradient; ii) diatom seasonality and taphonomy; iii) the determination of species optima and the variation of these optima between published datasets; iv) unvarying responses of diatom species assemblages to changing environmental conditions; v) the use of a single habitat in the development of diatom-based inference models; and vi) eutrophication and re-oligotrophication of UK lowland reservoirs.

9.2.1 Reconstruction of a single environmental gradient?

In the current study, the results of constrained and partially constrained CCAs on the UK lowland reservoirs dataset (Chapter 6) revealed that the measured environmental variables were able to explain a statistically significant proportion of variation in the diatom data. A high level of covariation was seen between measured environmental variables. However, variance partitioning of the full dataset illustrated that, although total phosphorus (TP) explained 5.5% of the variance in the species data, only 2.1% of this variation was explained solely by TP. The difference between these figures represents explanatory power derived from the covariation of TP and alkalinity (Alk), potassium (K) and secchi depth (SD). In contrast, the explanatory power of chlorophyll-*a* (Chla) was largely derived from

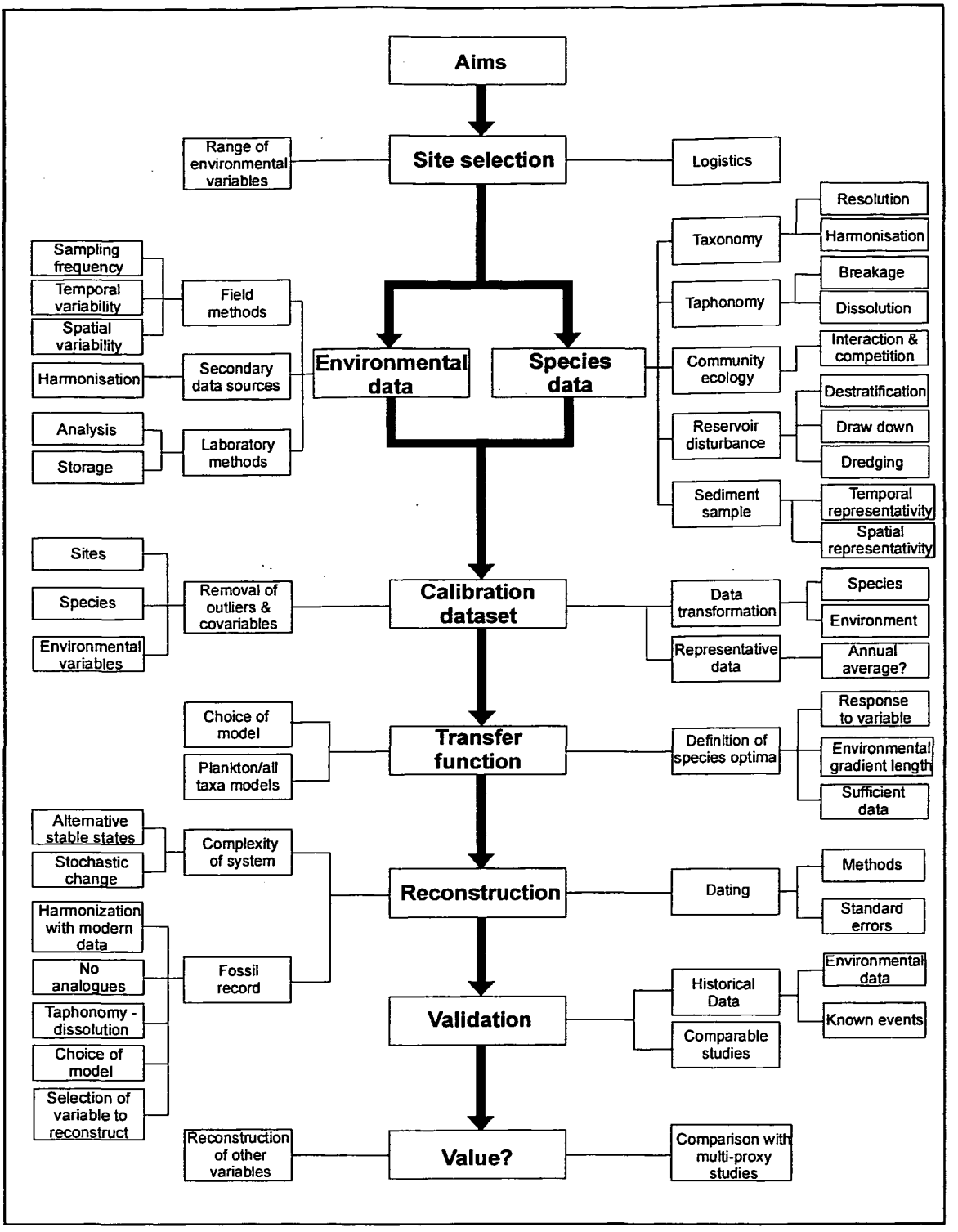


Figure 9.1 **Flow diagram illustrating the various phases in the development and application of inference models. At each stage decisions must be taken that impact upon subsequent stages, in turn influencing the overall outcome and value of the inference model approach in palaeolimnological research.**

its discrete influence. However in common with TP, the overall percentage of variance explained by Chla was low at 5.7%. Thus, despite the high statistical significance of the variation explained by the key measured environmental variables carried forward for

inference model development, there remained considerable residual variation unexplained by the variables measured in this study. It may therefore be unwise for palaeolimnologists to rely too heavily upon the reconstruction of a single environmental variable to explain ecosystem change. This highlights a key issue, namely that of "a multitude of organisms in environments with equally multitudinous factors all fluctuating seasonally" (Round, 1971, p.70).

The reconstruction of a single environmental gradient fails to take into account the multitude of elements impacting upon aquatic environments. Whilst overall phytoplankton productivity is positively correlated with increasing concentrations of nutrients (Dillon & Rigler, 1974; Smith, 1982; Prairie *et al.*, 1989; Gibson *et al.*, 1996), this appeared to be the only predictable consequence of increased trophic state in the UK lowland reservoirs calibration set. Phytoplankton community assembly is a complex process subject to considerable stochasticity. Reynolds *et al.* (2000) remark that; "there is no single axis of variability and there is no single relationship that will ever predict the floristic composition of the phytoplankton of a lake from the quantities of nutrient it receives" (p.149). Different phytoplankton assemblages can be observed in lakes with similar nutrient concentrations and similar assemblages can be found in lakes with differing nutrient concentrations (cf. Naselli-Flores, 2000). Over the last decade, there has been a distinct shift in the thinking of limnologists towards a more holistic view of plankton systems and their metabolism (Reynolds *et al.*, 2000). This move has been away from the Vollenweider-type approach (Vollenweider, 1975, 1976; OECD, 1982) founded on the principle that the availability of nutrients, in particular phosphorus, principally determines phytoplankton assemblage composition.

9.2.2 Taphonomy and diatom seasonality

As illustrated in Chapters 6 and 7, environmental variables exhibit a high degree of temporal variability, as do planktonic diatom assemblages. Inference models such as those created in the current study, rely on the surface sediment sample collected and analysed being an accurate representation of the diatom assemblage living in a particular site (cf. Roberts, 1998). Measures can to some extent be taken to reduce the impact of taphonomic processes such as dissolution, breakage and seasonal variability. By comparing the relationship between contemporary planktonic diatom data and surface sediment sample composition, Sayer (1997, 2001) highlighted the importance of the timing of sediment sampling on the presence of seasonal artefacts and decomposition / dissolution processes in recently sedimented diatom assemblages. Similar findings in the current study (Chapter 7)

confirm the importance of these observations. This highlights the need to consider the timing of surface sediment sampling and the importance of selecting the optimal 'slice' of surface sediment (e.g. 0-0.5 cm / 0.5-1 cm / 1-2 cm) to provide the most accurate representation of planktonic diatom population dynamics over the period when the associated environmental data were measured.

However, such methodologies usually have greater logistical requirements, and despite the extra time and effort afforded, may still fail to overcome the various taphonomic processes that can potentially occur between sedimentation of contemporary diatom assemblages from the water column and their subsequent transformation into the fossil record. Analyses in Chapter 6 indicated that there could be significant differences between live and fossil diatom assemblages. Therefore, whilst every effort should be taken to minimise the effect of taphonomic processes on the diatom assemblage data utilised in calibration datasets and inference models, it is perhaps also appropriate to accept that such differences exist and will ultimately affect the reconstructed values. More may be gained in attempting to understand the likely impact of taphonomic processes on the interpretation of results, than to presume that the effects of these inevitable processes can be fully overcome.

The combined study of modern ecological phytoplankton dynamics and palaeolimnology in UK lowland reservoirs may be more informative than using each approach in isolation. It may also be more informative to take an assemblage-based approach (e.g. Reynolds, 1984b), as opposed to treating taxa as individuals and assigning each with an environmental optimum. The differential loss of species due to taphonomic processes is less important if an assemblage-based approach is taken, since no individual taxon can drive the reconstruction. It is worth considering the results of ordinations when assessing species distributions and their relationships to environmental gradients. However, it should be noted that the location of an individual taxon in ordination space is dependent upon its relative abundance in each site. The current study thus supports a combination of quantitative (inference model) and semi-quantitative (ordination of species assemblages and environmental variables) approaches to the reconstruction of reservoir nutrient histories.

9.2.3 Species' optima – observations on consistency and robustness

The variation in species' optima derived from different calibration datasets

Table 9.1 presents the WA optima derived from various published datasets for selected species. There are expected to be some issues relating to taxonomic resolution and harmonisation between these datasets. Despite authors often documenting details of taxon

authorities, harmonisation between datasets is far from straightforward. In the process of compiling Table 9.1, some assumptions have been made regarding species delineations. For example, many of the medium to long pennate, finely striated *Fragilaria* spp. to which other authors refer, are termed *Synedra* spp. in this study e.g. *Fragilaria capucina* var. *gracilis* is taken as synonymous with *Synedra rumpens* var. *familiaris* and *Fragilaria capucina* var. *rumpens* is seen to be synonymous with *Synedra rumpens*. Whilst these assumptions may not be entirely correct, the inclusion of the taxa concerned maximises the utilization of ecological information in all datasets, highlights the variation between datasets and enables at least broad comparisons to be made.

Table 9.1 and Figure 9.2 reveal variations in the TP optima derived for selected taxa both in this study and in published datasets. It serves to provide a stark reminder of the limitations of the inference model approach, highlighting the broad tolerances of many species to ambient epilimnetic TP concentrations across different lake types and in different geographical regions. For example, seven different models derive diverse optima for *Aulacoseira granulata*. The models for S.E. Ontario lakes, UK lowland reservoirs and N.W. European lakes derive optima of 19 μgl^{-1}, 83 μgl^{-1} and 136 μgl^{-1} respectively. The highest optimum is derived from a dataset consisting predominantly of shallow lowland lakes, with a dataset TP mean of 104 μgl^{-1}. The lowest optimum is derived from a dataset consisting of relatively deep natural lakes, with a dataset TP mean which is considerably lower (14 μgl^{-1}). It follows that optima derived from datasets with high mean TP concentrations will necessarily be higher, with the converse true of datasets with low mean TP concentrations.

Six different models derive optima for *Tabellaria flocculosa*, ranging from 11 μgl^{-1} in Alaska, through 15 μgl^{-1} in S.E. Australian reservoirs, to 32 μgl^{-1} in UK lowland reservoirs. Most models derive similar optima for this taxon. The optimum of *T. flocculosa* in the current study appears to be overestimated because its distribution curve is truncated at the lower end (Figure 7.5a). The low TP sites where *T. flocculosa* occurred in the highest relative abundances were removed, due to their outlier status in Chapter 7. However their inclusion would not have lowered the TP optimum of *T. flocculosa* to concentrations as low as those derived by other datasets, since the lowest TP site in the UK lowland reservoir dataset had a TP concentration of 11 μgl^{-1}.

Species	WA optimum (**Denmark – shallow lakes**): 29 lakes range = 24 - 1145 µgl^{-1} TP; mean = 164 (Bradshaw *et al.*, 2001)	WA optimum (**NW Europe – shallow lakes**): 152 lakes range = 5 - 1192 µgl^{-1} TP; median = 104 (Bennion *et al.* 1996)	WA optimum (**EDDI – Combined**): 347 lakes range = 2-1189 µgl^{-1} TP; *mean* = 99 (Juggins *et al*, 2001)	WA optimum (**SE Australia - reservoirs**): 33 reservoirs range = 7 - 481 µgl TP^{-1}; mean = 66 (Tibby, 2004)	WA optimum (**UK lowland reservoirs**): 41 reservoirs range = 12 - 242 µgl^{-1} TP; mean = 63 (Burgess, this study)	WA optimum (**Sweden - lakes**): 43 lakes range = 7 - 369 µgl^{-1} TP; mean = 63 (Bradshaw & Anderson, 2001)	WA optimum (**Alps & pre-Alps**): 86 lakes range = 2 - 266µgl TP^{-1}; mean = 22 (Wunsum & Schmidt, 1995)	WA optimum (**British Columbia**): 59 lakes range = 5 - 85 µgl TP^{-1}; mean = 20 (Reavie *et al.*, 1995)	WA optima (**SE Ontario**): 64 lakes range = 4 – 540 µgl TP^{-1}; mean = 14 (Reavie & Smol, 2001)	WA optimum (**Alaska**): 51 lakes range = 3 - 84 µgl TP^{-1} (Gregory-Eaves *et al.*, 1999)
AchMin	-	37	25	25	48	34	15/19	14	16	12
ActNormS	-	-	-	151	130	-	-	-	-	-
AstForm	108	76	44	18	48	61	-	15	14	12
AulAmb	152	63	57	34	49	57	19	23	16	12
AulGrA	-	-	114	53	71	-	-	27	-	-
AulGr	-	136		49	83	51	52	36	19	-
AulIslan	-	70	33	-	102	44	13	-	-	-
AulSub	-	43	39	-	44	72	-	17	14	16
CycPseu	-	146	40	27	88	55	-	-	13	9
CycRad	-	36	27		48		18	11	10	
CycsCfTh	241	217	214	76	76	-		22	20	
CycsDub	201	175	153	62	82	64	-	-		-
CycsInv	497	236	206	-	94	-	-	-	-	-
DiatTenE	-	88	73	31	52	66	8	14	19	
FraCapM	-	162	131	-	76	-	-	16	27	50
FraCrot	97	105	31	12	50	62	15	18	14	21
NitzPal	-	144	80	69	92	-	13	18	16	17
StAlp	-	69	15		70		10	12	19	
StHantz	251	224	190	-	71	74	-	14	24	-
StHantzT	-	-		-	103	-	111	15	22	
StNeo	-	125	68	-	93	-	18	-	-	-
StParvus	158	131	69	46	62	125	27	17	28	19
SynAcA	-	75	55	-	45	-	15	-	-	-
SynAcR	-	28	24	-	43	-	-	11	-	14
SynRuFa	-	-	22	12	28	-	16	-	15	18
SynRump	-	64	33	28	65	-	17	-	-	21
TabFloc	-	13	15	15	32	-	-	18/23	12/13	11

Table 9.1 **Comparison of WA optima derived from various published datasets for selected taxa. Species are ordered alphabetically. For the key to taxon codes, see Appendix 3.**

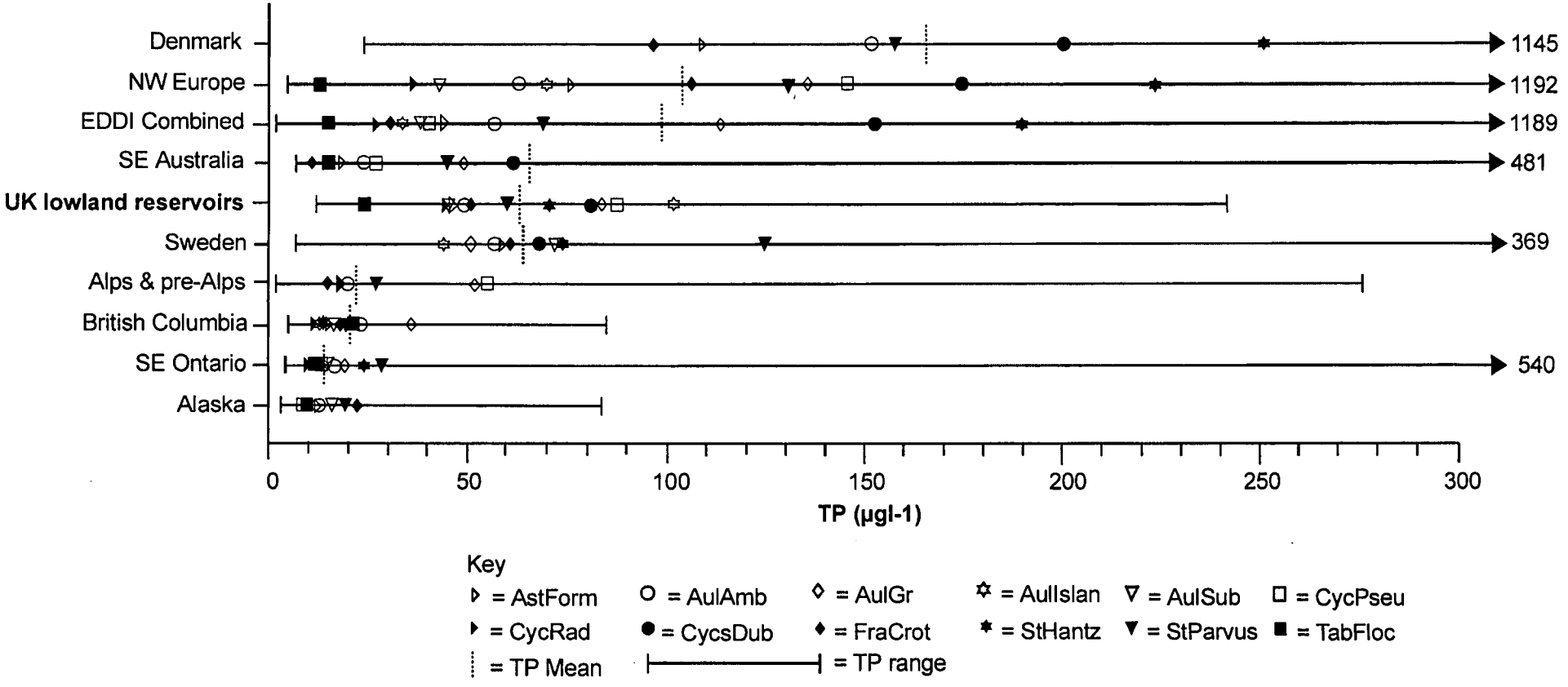


Figure 9.2 Comparison of the TP WA optima for selected species from various published datasets. For further details of datasets see Table 9.1, for species codes see Appendix 3.

Figure 9.2 clearly illustrates that the estimated WA optima and tolerances of individual diatom taxa are dependent upon the lower and upper limits of the environmental gradient sampled and are therefore best considered as relative to the other taxa in the dataset rather than as absolute values. This is clearly displayed in those sites with short TP ranges; in such sites optima must be lower and less widely distributed than in studies with high TP ranges. Since species abundance is partly a function of seasonality and competitive interactions, optima determined for individual taxa are dependent not only upon the sites included in the calibration set, but also upon the timing of water chemistry (Bennion & Smith, 2000) and surface sediment (DeNicola, 1986; Sayer, 1997, 2001) sampling.

The ecological relevance of species' optima

The variation in individual species' optima derived from different calibration sets exemplifies the fact that the inference model approach is based on a 'black-box' statistical methodology, rather than on a fundamental understanding of the processes mediating the relationship between species abundance and individual environmental variables, such as TP. Figure 9.2 highlights the assertion that many of the mechanisms linking species and TP at any one site are, at least in part indirect. Such indirect factors may include competitive species interactions or the effect of turbidity and artificial destratification. Therefore the definition of WA optima in one calibration set site, or set of sites, and the consequent application of these optima to other sites in the form of an inference model, may not provide 'real' ecological information. Thus despite the reported robustness of DI-TP inference models and the high degree of certainty within which optima can be defined (Hall & Smol, 1999), species' optima may be "ecologically naïve" in that they do "not really represent the 'optimal' nutrient levels for the species' growth (if such a level exists)" (Bradshaw & Anderson, 2002). It would seem fair to conclude that there is no universally applicable, 'absolute' relationship between the growth preferences of individual diatom taxa and variations in specific environmental conditions. Although controlled laboratory experiments (e.g. Kilham, 1971), and in-lake experiments (e.g. Lund tubes, Reynolds *et al.*, 1983, 1984), can to some extent provide a more ecologically relevant approach to defining the optimal growth conditions and tolerances of individual taxa, their applicability outside controlled experimental conditions is often questionable.

The importance of accurate definition of species' optima for the distinction between ecologically important and stochastic shifts in diatom species assemblages

The accurate definition of species optima is vital for the creation of effective diatom-based WA inference models. For reconstruction purposes it is suggested that sufficient species

data should be available to set robust optima for different diatom assemblages occurring under the same TP concentrations. If this is the case, then the occurrence of divergent diatom species assemblages under similar TP concentrations should not greatly affect the overall reconstructed values. Figure 9.3 illustrates the impact of shifts in species assemblages upon DI-TP reconstructions. If species optima are well defined, then inter- and intra-annual stochastic changes in diatom species assemblages should not influence reconstructed nutrient status (Figure 9.3a). Ecologically important switches in species composition from assemblages indicative of mesotrophic conditions to those indicative of eutrophic conditions should generate an increase in inferred TP concentrations (Figure 9.2b). Conversely, if species optima are poorly defined then a stochastic change in species composition may result in anomalous reconstructions inconsistent with measured values (Figure 9.2c), whilst real changes in nutrient conditions may be masked (Figure 9.2d).

In Chapter 8, historic changes in Blackbrook reservoir's TP concentrations were reconstructed using both the UK lowland reservoirs TP inference model and the EDDI Combined TP model (Juggins *et al.*, 2001). The reconstructions under both models followed similar trends throughout most of Blackbrook's history. However, the increasing relative abundance and subsequent dominance of *Aulacoseira islandica* resulted in a divergence in the trends reconstructed by the different models. The EDDI model indicated no change in TP concentrations following the shift towards *A. islandica*, which could indicate either scenario a) or d) in Figure 9.3. Conversely, the UK lowland reservoirs model reconstructed a significant increase in TP concentrations with this species shift, which could indicate either scenario b) or c) in Figure 9.3. It is unclear which of these reconstructions is most trustworthy. The absence of long-term TP data and an uncertain core chronology make the task more difficult. The EDDI model WA optimum for *A. islandica* is based on a suite of natural lakes. It is possible that the optimum for this taxon in natural lakes is inconsistent with that in reservoirs. Therefore when this optimum is applied to the *A. islandica*-dominated section of Blackbrook's stratigraphy, reconstructed TP concentrations may be underestimated, thus masking any genuine increase in trophic status (synonymous with Figure 9.2d. However in the UK lowland reservoirs calibration set, *A. islandica* is present in the surface sediments of only four reservoirs and therefore its optimum may have been poorly defined. The reconstruction of Blackbrook's trophic status according to the UK lowland reservoirs calibration set could therefore indicate a shift in nutrient concentrations in the absence of any real change during the period of *A. islandica* dominance. This would be synonymous with Figure 9.3c.

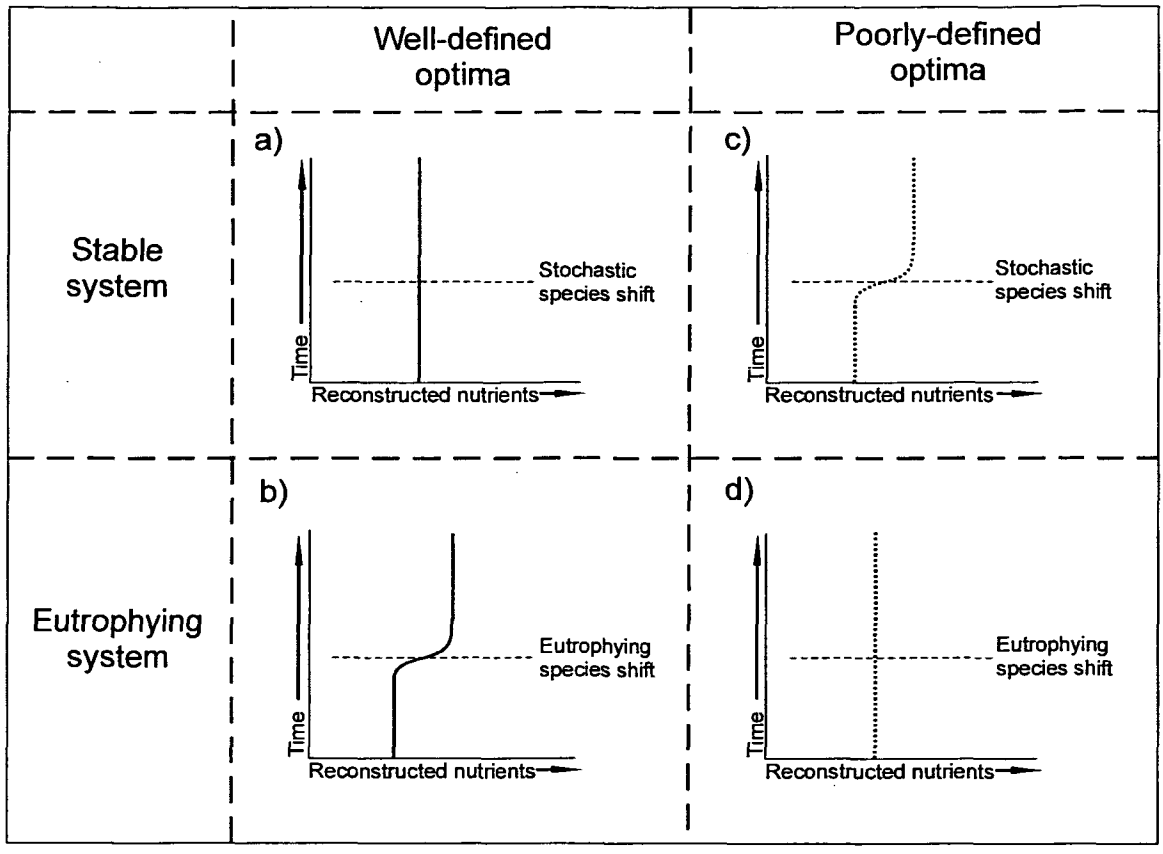


Figure 9.3 **Conceptual representation of the influence of the robustness of diatom species optima on interpretation of species shifts under stable and perturbed conditions. Simplified diagrams represent a single change in species and its possible influence on diatom-inferred nutrient reconstructions. Where optima are well defined, stochastic changes do not affect reconstruction (a) but eutrophying changes do (b). Where optima are poorly defined, stochastic changes may affect reconstructions (c), but eutrophying changes may be masked (d).**

Habitat heterogeneity and its influence on the definition of species' optima

TP reconstructions from shallow lake ecosystems frequently suffer similar problems from poorly defined optima, although these problems appear to be largely related to habitat heterogeneity (Bennion, 1994, 1995; Bennion *et al.*, 2001; Sayer, 2001). For example, the dominance in many shallow lakes of the cosmopolitan and broadly nutrient tolerant small, benthic *Fragilaria* spp. results in unrealistic nutrient trajectories with a lack of sensitivity to nutrient enrichment (Sayer, 2001). In shallow lakes, the balance of diatom habitats e.g. the extent of macrophyte coverage or the availability of illuminated bottom sediments, may be more important than nutrient concentrations in determining observed species assemblages. For example in Groby Pool, Leicestershire, Sayer (2001) observed an increase in the relative abundance of the epiphytic taxon *Cocconeis placentula*, which was associated with an increase in the biomass of submerged macrophytes consequent upon eutrophication. However, when the S.E. England shallow lakes inference model (Bennion, 1994) was

applied, the relatively low optima assigned to *C. placentula* implied a decline in DI-TP as this taxon increased in relative abundance. In UK lowland reservoirs, the problem of habitat heterogeneity is largely avoided due to the dominance of one main habitat - the plankton. However the full suite of 26 environmental variables measured in the current study together explained approximately 65% of the variance in the diatom species data and the variables for which inference models were developed (TP, Chla and EC) each accounted for only 5-7% of the variance. Therefore the effects of other unmeasured variables, such as zooplankton grazing, morphometry, retention times and circulation patterns, alongside the impact of inherent environmental stochasticity may have thwarted the interpretation of observed species shifts that were unaccounted for by diatom-inferred reconstructions of single environmental variables.

Accounting for different taxon-environment distributions and species' tolerances in the development of inference models

The very nature of the inference model approach requires that an environmental optimum is assigned to each individual diatom taxon even if it shows no clear relationship to the variable in question. Many of the most dominant planktonic taxa in the UK lowland reservoirs calibration set showed a broad tolerance and/or no clear response to TP. Only 35% of taxa in the full dataset and 41% of taxa in the planktonic diatom dataset showed unimodal responses to TP. This raises issues about the robustness of TP optima defined using weighted averaging (WA) techniques, which assume that all taxa show unimodal responses. Broad tolerance is indicative of ubiquitous taxa whose distributions are unlikely to be affected by environmental change. Racca *et al.* (2003) demonstrated that for weighted averaging partial least squares (WAPLS) models, performance steadily improved as taxa with broad tolerances were removed. Further they noted that taxa with a broad tolerance were essentially the taxa with a sigmoidal response curve as opposed to a unimodal response. This indicates that inclusion in inference models of taxa with both broad tolerances and non-unimodal responses to an environmental variable may inhibit the usefulness of WAPLS techniques in making environmental inferences. Thus there is an argument for focussing on those taxa with narrow environmental tolerances, which may be of greater rarity in the calibration dataset as a direct consequence of their specialised environmental preferences and hence narrower tolerance ranges (cf. Philibert & Prairie, 2002a). This is almost synonymous with the 'indicator species' approach used in early palaeolimnological studies of eutrophication.

Artificial neural networks (ANN) present a different statistical modelling technique to WA approaches (Lek *et al.*, 1996; Racca *et al.*, 2001, 2003). The main advantage of ANNs is that no prior assumptions about the relation between independent and dependent variables are necessary and, unlike WAPLS and PLS models, they do not assume either unimodal or linear responses of all taxa. ANNs therefore have the potential for modelling and incorporating mixtures of taxon responses (Birks, 1998), although they have yet to be fully explored in quantitative palaeolimnology. In relation to diatom-based pH inference models, Racca *et al.* (2001) stress that WAPLS and ANN models are complementary. Since they are different in the taxon information used in their prediction, each model is capable of capturing a part, but not all, of the underlying complex relationships between diatom assemblages and pH. It is therefore suggested that "the development of dual models, based on the average results of both WAPLS and ANN" may be necessary "to obtain more reliable and robust reconstructions" (Racca *et al.*, 2001 pp.419-420).

The role of environmental gradient length and calibration set geographical coverage in the definition of species' optima

To increase the probability of well-defined optima, it is usually suggested that calibration sets should straddle long environmental gradients (Hall & Smol, 1999). However there is also an argument for using shorter environmental gradients by creating dynamic calibration sets and applying linear-based techniques such as partial least squares (PLS) over shorter sections of the overall environmental gradient (Birks, 1998). This could minimise the undesirable 'edge effects' inherent in unimodal-based methods involving weighted-averaging estimation (Hill & Gauch, 1980; ter Braak & Juggins, 1993), in turn improving the calibration models created.

Birks (1998) suggests that a possible solution to the problem of poorly defined diatom species optima, would be to "extend the geographical and environmental coverage of modern calibration datasets by carefully combining data and yet retaining their taxonomic quality and integrity" (Birks, 1998, p.316). This could take the form of a world-wide 'super' calibration set with consistent taxonomy and associated measured environmental variables. According to Birks (1998), such a dataset could be subjected to modern analogue technique (MAT) analysis for the selection of 10 to 20 modern samples that are most similar to *each* of the fossil samples, which would in turn form a bespoke calibration set specific to the fossil sequence under reconstruction. This approach is analogous to development of the EDDI Combined TP calibration dataset (Juggins *et al.*, EDDI website). However the EDDI dataset is restricted to European lakes and includes heterogeneous lake typologies. It

comprises few reservoirs and as a result some taxa common in UK lowland reservoirs, for example *Actinocyclus normanii* fo. *subsalsa*, have 'no-analogues' in the calibration dataset. However, as illustrated in Chapter 8, when Blackbrook reservoir's past TP concentrations are reconstructed, the EDDI Combined TP model appears to help overcome the 'no-analogue' problem encountered in core sections dominated by *A. islandica*.

Birks (1994) stresses the importance of taxonomic precision for palaeoenvironmental reconstructions, making the point that there is "no substitute for good data and such data invariably implies the need for a sound and detailed taxonomy" (p.116). However Stoermer (2001) highlights the present chaotic state of diatom taxonomy. A major issue with the development of all-encompassing worldwide calibration sets is the harmonisation of taxonomy and environmental variables between datasets. As calibration sets expand, this issue is expected to be of increasing concern and must be overcome if best use is to be made of the fine-scale taxonomic resolution often employed by individual diatom palaeolimnologists. Loss of distinction between different species and morphotypes may result in loss of ecological information, particularly where close correlation between morphology and ecological range has been demonstrated (e.g. Cox, 1994; Håkansson & Korhola, 1998; Denys *et al.*, 2002). Recognition of taxa with restricted ecological ranges can improve the predictive power of diatoms in water quality monitoring and palaeolimnological studies (Anderson *et al.*, 1993). Conversely, taxa with wide ecological preferences are usually considered of poor indicator value (e.g. Philibert & Prairie, 2002a).

Typology-specific calibration sets and inference models

One way in which it may be possible to overcome the problem of extensive data harmonisation is to create a typology-specific e.g. a reservoirs calibration dataset. This could be developed by amalgamating reservoir datasets from around the world (e.g. Tibby, 2004). Although data harmonisation would still be necessary, it would be on a much smaller scale and thus its development would require fewer resources. Taxa such as *Actinocyclus normanii* fo. *subsalsa* and *Aulacoseira subarctica* fo. *subborealis* are common in the Australian reservoir dataset of Tibby (2004) which should help to improve the estimation of optima for these taxa for WA approaches, whilst extending the range of possible modern analogue sites for MAT analysis. However, factors such as endemism should be considered when amalgamating datasets from disparate geographical regions.

9.2.3 Unvarying responses of diatom populations to TP

Another problem with the inference model approach is that species may cease to respond to changes in the variable under reconstruction. This may be problematic particularly towards the ends of the environmental gradient, where factors other than that under reconstruction may become more important in determining species distributions. To enable investigation of this issue Figure 9.4 illustrates the DCA axis 1 scores plotted against mean annual epilimnetic TP and Figure 9.5 displays the diatom taxa occurring in the surface sediments of the UK lowland reservoirs calibration dataset. Sites are ordered according to mean annual measured TP concentrations and species are ordered according to TP WA optima (full model). The surface sediment diatom species data (square root transformed, all taxa included) was separated into zones using a stratigraphically constrained (according to TP) hierarchical cluster analysis CONISS (Grimm, 1987).

Zones 1-5 in Figure 9.5, comprise reservoirs with mean annual TP concentrations of <70 μgl^{-1}. These reservoirs show relatively low, but greatly fluctuating DCA axis 1 scores (Figure 9.4). Zones 1-4 comprise sites with TP concentrations <32 μgl^{-1} and constitute half of the eight zones identified by CONISS, suggesting that there is considerable change in the composition of diatom species assemblages at TP concentrations of <32 μgl^{-1}. This may partly reflect the higher sensitivity of aquatic ecosystems to small changes in TP concentrations at the lower end of the TP gradient (e.g. Jones *et al.*, 1997; Bennion *et al.*, 2004). At lower TP concentrations it appears that many different combinations of diatom species can grow successfully in the dynamic and plentifully supplied temporal and spatial niches. As concentrations of TP steadily increase, so the colonisation opportunities in both time and space diminish, as fewer and fewer diatom species are able to compete successfully against other algal species. Only the highly competitive 'opportunist' or 'coloniser' diatom taxa are able to survive. It is possible that in high TP sites, as the growth niches of diatoms are gradually 'squeezed' into smaller areas and shorter seasons, the numbers and biovolumes of diatom populations will decrease (cf. Blackbrook reservoir, this study).

The division between Zone 4 and Zone 5 approximately coincides with the change from mesotrophic to eutrophic status according to OECD (1982) criteria, providing some support to the division in trophic state classification at this TP concentration. There appears to be a clearer distinction at 32 μgl^{-1} TP than at 70 μgl^{-1} in terms of the occurrence of certain diatom taxa. For example, *C. dubius*, *A. granulata*, *A. granulata* var. *angustissima* and *S. hantzschii* fo. *tenuis*, are far more prevalent, or only occur in Zones 5-8. All the

aforementioned taxa are reported to be common in anthropogenically disturbed lakes and rarely occur in unperturbed systems (e.g. Bennion, 1994; Bradshaw, 2001; Kauppila *et al.*, 2002). Similarly, *T. flocculosa* only occurs in reservoirs with TP concentrations <45 μgl^{-1}, but is most prevalent in sites with <20 μgl^{-1} TP. A decline in *T. flocculosa* is a well-documented symptom of eutrophication (Reynolds & Irish, 2000). For example, the diatom stratigraphy from Lake Valkjärvi, Finland (Kauppila *et al.*, 2002), documents the demise of *T. flocculosa* over reconstructed TP concentrations of between 20 and 40 μgl^{-1}. This supports the observations from the current study and appears to indicate that ~30 μgl^{-1} is an ecologically important threshold concentration of TP, where ecosystem change may occur as a result of cultural eutrophication.

At ~70 μgl^{-1} TP, there is a shift towards higher DCA axis 1 scores (Figure, 9.4), which remain high until ~100 μgl^{-1} TP. This coincides with Zone 6 in Figure 9.5, typified by shallow, turbid reservoirs, in which *C. dubius*, *A. subarctica* fo. *subborealis* and *S.* cf. *agassizensis* occur at moderate to high relative abundance. These taxa are all indicative of increased nutrient loadings (e.g. Anderson, 1997; Bradshaw & Anderson, 2001; Bradshaw & Anderson, 2002; Denys *et al.*, 2002).

At ~100 μgl^{-1}, there is a significant shift from high fluctuating to low fluctuating DCA axis 1 scores (Figure 9.4). This coincides with the division between Zones 6 and 7 in Figure 9.5 and also coincides with the division between eutrophic and hypertrophic classifications according to OECD (1982) criteria. Zone 7 comprises sites with TP concentrations ranging from 99-135 μgl^{-1} and consists predominantly of impounding reservoirs. The species assemblages of these reservoirs are dominated by a combination of *A. granulata* and *F. crotonensis,* or alternatively *A. formosa* and the percentage of planktonic taxa in this zone is consistently high. These sites are generally artificially destratified, which may explain the prevalence of *A. granulata* and *F. crotonensis*, whose growth is reported to benefit from turbulence (Bailey-Watts *et al.*, 1986; Steinberg & Gruhl, 1992; Lindenschmidt & Chorus, 1997; Reynolds & Irish, 2000). Increased turbulence of the water column throughout the year may also help to explain the presence of *A. formosa* in some sites in this zone, in contrast to its more frequent occurrence and overall higher relative abundance in sites with lower mean annual TP concentrations.

In the UK lowland reservoir calibration set, it appears that there is little change in diatom species composition above ~135 μgl^{-1} TP, illustrated in Figure 9.4 by constantly high DCA axis 1 scores. This is further exemplified in Figure 9.5, where the first CONISS division

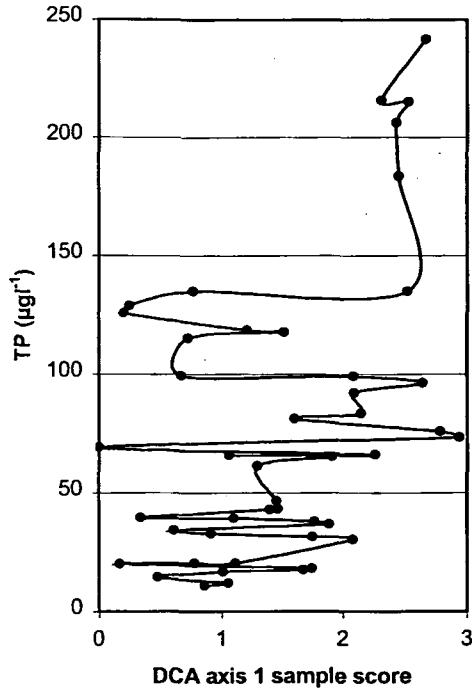


Figure 9.4 **DCA axis 1 sample scores plotted against mean annual epilimnetic TP for the 46-reservoir calibration set. Grafham is omitted, however the trend would continue in a straight vertical line to this site at >600 µgl $^{-1}$ TP.**

(between zones 7 and 8) is made in the surface sediment species data. All sites in zone 8 are pumped storage facilities, with mean annual TP concentrations >135 µgl^{-1}. According to Anderson *et al.* (1993), diatom species composition changes little as P concentration increases above 100-200 µgl^{-1} TP. Similarly Reavie *et al.* (1995) suggest that there is little change above ~80 µgl^{-1} TP. This range of TP concentrations may reflect a critical level above which diatoms are unable to structurally respond to further increases in TP (Bennion, 1995). As a consequence, a stable diatom population structure is maintained, consisting of species with efficient growth strategies at both low Si:TP and TN:TP ratios and higher water temperatures (e.g. *K*-strategist diatom taxa with larger surface area to volume ratios such as *C. meneghiniana* (Tilman *et al.*, 1982; Tibby, 2004) and those of the *Stephanodiscus-niagarae*-complex e.g. *S. neoastraea* (Harris *et al.*, 1983; Stoermer *et al.*, 1985). TP is generally considered to be the primary limiting nutrient affecting algal growth in lakes. However, as TP increases to the critical level of ~135 µgl^{-1} in UK lowland reservoirs, other factors such as limitation of Si and/or TN, and the influence of turbulence may be of increasing importance (see Chapter 6 and 7), perhaps helping to explain the linear response to TP above a concentration of ~135 µgl^{-1}.

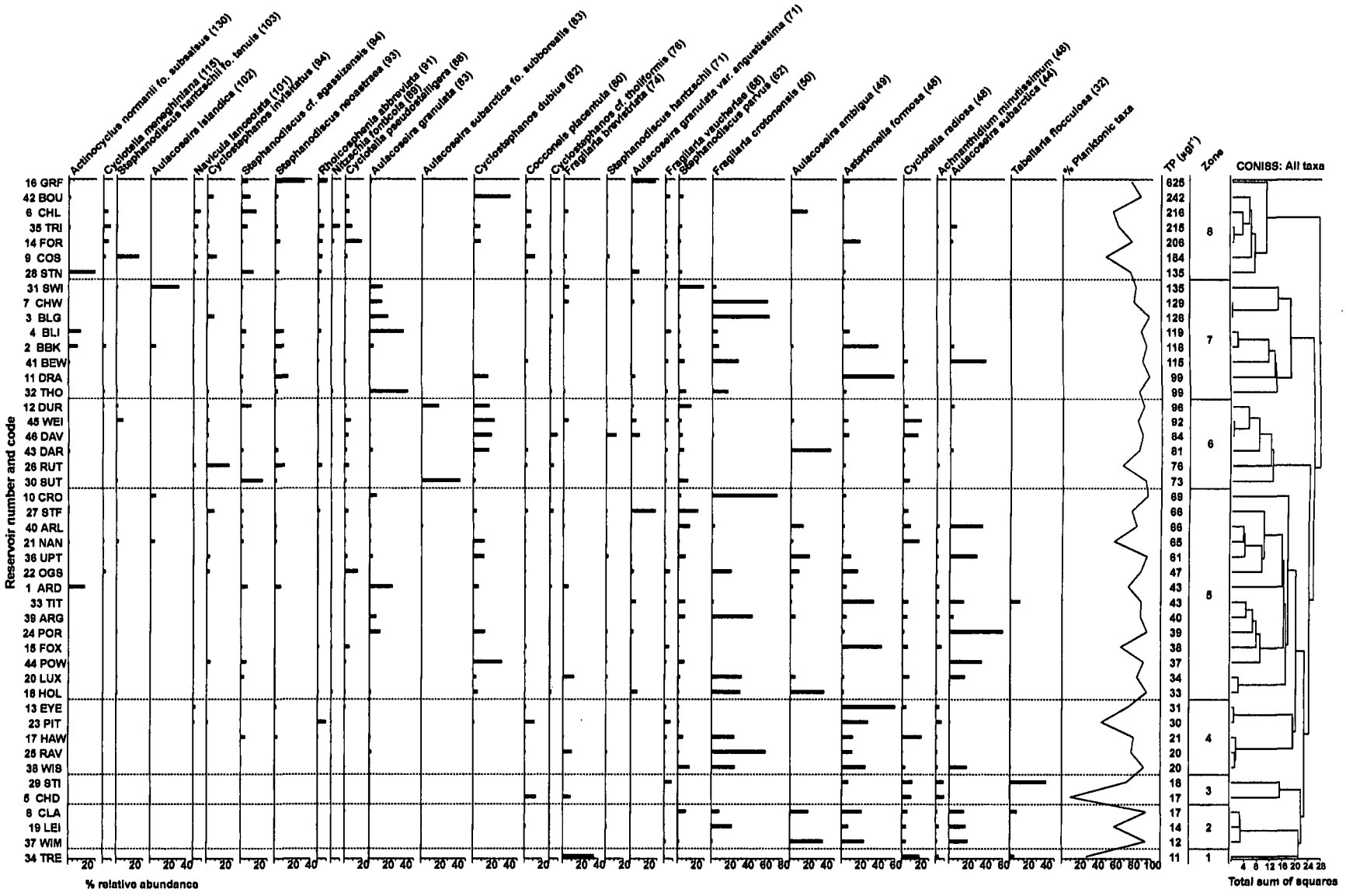


Figure 9.4 Percentage relative abundances of selected diatom taxa in the surface sediments of the 46-reservoir training set. Species are ordered from highest to lowest WA optima (in brackets) and sites are ordered from highest to lowest mean annual TP, (only taxa occurring with ≥5% relative abundance in one or more samples are shown).

Alternatively for this UK lowland reservoir dataset, the driving force determining the constant composition of surface sediment diatom species assemblages may occur because all reservoirs with TP concentrations >150 μg l^{-1} TP are pumped storage facilities. The majority of inflow water entering these sites is sourced from large rivers, which appears to affect the composition of diatom species assemblages. The species in these pump-storage reservoirs may to some extent be an artefact of river water populations, which do not generally occur in natural lakes but often occur in reservoirs when innocula are supplied from inflowing river systems. Many of the diatom species found in the hypertrophic pumped storage reservoirs in this study are reported to be prevalent in eutrophic / hypertrophic rivers. For example, *Cyclotella meneghiniana*, *Stephanodiscus agassizensis* (Kiss & Genkal, 1993), *Actinocyclus normanii* (Kiss *et al.*, 1990), *Aulacoseira granulata* (Hötzel & Croome, 1996) are all found in nutrient-rich lowland rivers. Two sites further evidence this; Staunton Harold, a pumped storage reservoir, and Swithland, an impounding reservoir, which have the same TP concentration, but differing surface sediment diatom species assemblages and are thus located either side of the first CONISS division in Figure 9.5. This may support the observations of Reynolds (1999) and Naselli-Flores (2000), that different diatom assemblages can occur at the same TP concentrations in different reservoirs as a result of the overriding influence of other constraining factors such as differences in hydraulic regime.

The observation of an unvarying response of diatom assemblages to TP concentrations above a critical level may indicate that it is inapt to include in trophic state inference models, reservoirs that further extend the range of TP, because DI-TP will most likely underestimate observed TP. It is probable that above concentrations of 100-150 μg l^{-1} TP, diatom species responses are indirectly related to nutrient availability, for example through the influence of light availability and turbidity. Efforts might therefore be better directed towards the response of alternative biological indicators e.g. other algal species (e.g. King *et al.*, 2000) or organisms such as chironomids (e.g. Prat & Daroca, 1983; Walker *et al.*, 1991; Sadler & Jones, 1997; Brooks *et al.*, 2001; Ruse, 2002) which respond to TP concentrations above 150 μgl^{-1}. Alternatively, as suggested in the WFD, attention might be better focused on a range of groups at different levels in the food chain e.g. protozoa, diatoms, other algae, macrophytes, invertebrates and fish. The combined biological indicator value would be expected to provide a better indication of the ecological status of a water body. Such 'multi-proxy' approaches have largely been confined to shallow lake environments (e.g. Brenner *et al.*, 1999; Sayer *et al.*, 1999), although examples do exist from deeper lakes (e.g. Lotter *et al.*, 1998; Birks *et al.*, 2000; Lotter, 2001). The results of such studies are encouraging and

environmental reconstructions based on different proxies are often complementary and rarely contradictory.

In terms of evolutionary ecology, fewer species appear to have evolved to exploit high TP environments. It is possible that species are constantly evolving strategies to cope with changing environments such as increasing nutrient concentrations. Jewson (1992) proposed that *Stephanodiscus* is evolving rapidly and Anderson (1995b) suggested that this could explain the plethora of new species and morphotypes described from the genus in the latter part of the 20th century, many of which have been shown to display different ecological tolerances (Theriot *et al.*, 1988; Håkansson 2002). The results of the current study support this view, since particular subspecies and morphs of both *Stephanodiscus* spp. and many other planktonic diatom taxa were often found to have restricted ecological ranges (e.g. *A. subarctica* fo. *subborealis*).

9.2.4 Comparison of inference models based on plankton and all taxa

Typically the waters of UK lowland reservoirs are of sufficient depth for the development of diatom assemblages dominated by taxa residing for the most part within the plankton. Even in the shallowest sites (~5m max. depth), water clarity is usually insufficient for the development of an extensive periphytic flora and similarly, the plankton is the dominant habitat available for diatom growth. The commonly occurring problem of dominance by ubiquitous non-planktonic *Fragilaria* spp. in the sediments of many shallow lake ecosystems (e.g. Bennion 1994, 1995; Jones & Juggins, 1995; Bennion *et al.*, 2001; Sayer, 2001) does not present an issue for the development of diatom-based inference models in UK lowland reservoirs.

Comparison of goodness-of-fit statistics for models using only planktonic, only periphytic, and all taxa is recommended by Siver (1999) to provide the most appropriate means to evaluate effectively the use of each habitat group in the construction of inference models. However, in respect of the lowland reservoir DI-TP model, low concentrations of periphytic diatom taxa in all but a handful of sites deems construction of a periphytic model inappropriate. Also, many periphytic taxa have lower TP, Chla and EC optima than planktonic taxa, reflecting their prevalence in reservoirs at the lower end of the calibration dataset range. Therefore it may be advantageous to include both periphytic and planktonic taxa in inference models because a decrease in periphytic taxa can reflect an early habitat shift as the bottom of the reservoir ceases to lie within the euphotic zone (Burgess, 1998; Sayer, 2001).

Plankton-only models created in this study and by Siver (1999) can only reliably be used to make inferences about lakes with diatom assemblages containing primarily (e.g. >50%) planktonic species. In common with Siver (1999), the number of reservoirs dominated by periphytic taxa was low and these sites were removed from the dataset prior to model construction (only 4 out of 46 (9%) reservoirs had <50% planktonic diatoms in the surface sediments and only 13 out of 46 (28%) had <75% planktonic diatoms). Bradshaw & Anderson (2001) made counts of >400 planktonic diatoms from all lakes. This was time-consuming in that large counts had to be made for non-plankton dominated lakes, but this methodology enabled all lakes, whether plankton or periphyton-dominated, to be included in the model. However in the current study, reservoirs where periphytic diatoms dominated were generally acidic, transparent or shallow, and it may not be valid to apply the plankton-based models generated in this study to such sites because there are probably factors relating to habitat heterogeneity that are more important than epilimnetic water chemistry in determining diatom species distributions. Such factors could include the availability of substrate for attachment, light penetration (Sayer, 2001) and inorganic and organic substances leached from macrophytes (Allen, 1971).

The plankton-only models developed in this study employ approximately half the number of species included in the full model (38 as opposed to 82). However, the performance statistics of the plankton-only models are much more than 'half as good' as those generated under the full model. This probably arises because, in general, UK lowland reservoirs provide a predominantly planktonic habitat and the surface sediments are therefore dominated by planktonic diatom taxa (~70%). Therefore although the plankton-only models do not perform quite as well as the full models, the differences are only slight and indicate that when calibration set sites are dominated by planktonic diatom species, plankton-only models may be adequate. Thus the development of plankton-only inference models is fully supported and justified. However there may be drawbacks with the use of such a reduced calibration dataset. The smaller number of taxa could affect the strength of the inference models, especially if many of the study lakes become dominated by fewer species. Moreover, the reduction in Hill's N^2 estimate could affect the estimation of species optima using weighted averaging, resulting in larger RMSEP estimates (ter Braak & van Dam, 1989; Birks *et al.*, 1990).

Cameron *et al.* (1999) reported that pH inference models based on all taxa showed the lowest RMSEP and bias statistics, suggesting that the rare taxa were contributing important

ecological information rather than introducing statistical 'noise' or random variation into the model. Philibert & Prairie (2002b) compared models based on planktonic, non-planktonic and all taxa. The outcome of their research recommended including all taxa in models, since this was found to yield the lowest prediction errors. Also, predictive errors could be further reduced by only including taxa exhibiting both a clear relationship and a narrow tolerance for the respective environmental variable. Large, species-poor diatom blooms frequently dominate plankton assemblages. If these taxa show a poor response to the selected environmental variable, then it may be appropriate to increase the count until sufficient data have been collected (e.g. ~ 400 valves) on the more responsive species, which should in turn improve inference model performance. This would be analogous to increasing the count of non-*Fragilaria* taxa in shallow lake systems, as discussed by Bennion (1995) and Sayer (2001) but this has only occasionally been carried out (Burgess, 1998; Bradshaw & Anderson, 2001).

Calibration datasets in palaeolimnology often contain few lakes but many taxa, leading to problems with "the curse of dimensionality" (Jongman *et al.*, 1995). This manifests itself in inference models that typically overfit the relationship between taxon assemblages and environmental variables, which is only partly overcome by procedures such as jackknifing that enable the generation of more realistic measures of predictive power (Racca *et al.*, 2003). In order to achieve maximum robustness, dimensionality i.e. the ratio of taxa : lakes must be as low as possible. Racca *et al.* (2003) stress that increasing the number of lakes in a calibration set inevitably leads to an increase in the number of taxa. Thus it may be more appropriate to reduce the number of taxa included in the model. Although inclusion in the model of as many taxa as possible decreases the probability of 'no analogues' when applied to fossil sequences, the effective relevance of individual taxa will vary depending on the environmental variable of interest. Using the Back-Propagation modelling approach of Artificial Neural Networks (ANNs), Racca *et al.* (2003) employed an ANN pruning algorithm to determine the functionality of individual taxa in terms of model performance to address the question of what diatom taxa to include in a modern calibration set. They found that for the Surface Water Acidification Project (SWAP) pH-diatom-dataset (Birks *et al.*, 1990), 85% of the diatom taxa could be removed without any effect on the pH model calibration performance. The removal of redundant taxa also improved the robustness (ratio of RMSE to RMSEP) of the calibration but did not affect measures such as Hills N^2 or tolerance. Although the plankton-only models created in the current study failed to improve upon the full model in terms of performance and robustness, the models performed only slightly less well.

The use of only one habitat group and the identification of fewer taxa to species level should reduce the time and effort required to develop inference models. Plankton-only models may therefore be more easily developed and employed by reservoir managers for the assessment of ecosystem change. However in common with the observations of Bradshaw & Anderson (2001) in Scandinavia, current phytoplankton monitoring in the UK by both water companies and the Environment Agency employs methods that classify planktonic centric diatoms into <10 μm and >10 μm diameter groups and not to species level. Thus it is likely that considerable ecological information is lost, in a similar way to the loss of information resulting from species harmonisation in the creation of large combined calibration datasets. Without maximising this information, a potential tool for the interpretation of environmental reconstructions may be lost.

9.3 Two axes of variation and the origins of divergence

Two axes of variation exist in the species and environment data, as shown by the CCA ordination diagram in Chapter 5. The first is a water chemistry gradient representing both nutrient and ionic concentration, whilst the second is a water clarity gradient, which in part reflects algal productivity. In contrast to much of what is described in the literature, UK lowland reservoirs do not exhibit a strong relationship between nutrient concentrations and algal productivity (Figure 4.7). The diagram illustrated in Figure 9.6 conceptualises the deviations that some reservoirs show from the expected linear relationship between nutrient concentrations and productivity. Many sites such as Cropston, Thornton, Stanford and Eyebrook follow the expected trend i.e. in the same trophic class (OECD, 1982) for both TP and Chla/SD. Other sites however diverge from the expected trend. The divergence appears to follow two distinct pathways. The first is typified by reservoirs supporting a lower productivity than might be expected from their nutrient state. The second shows the inverse trend, with higher productivity than expected from measured nutrient concentrations.

High nutrient concentrations but lower than expected productivity

Those sites with high nutrient concentrations but lower productivity levels than expected comprise deep pump-storage reservoirs that employ artificial destratification techniques to prevent stratification and in turn control phytoplankton growth rates. Examples of such reservoirs include Grafham, Pitsford, Ogston and Foremark. Lower productivity in these water bodies appears to be related to the impact of artificial destratification.

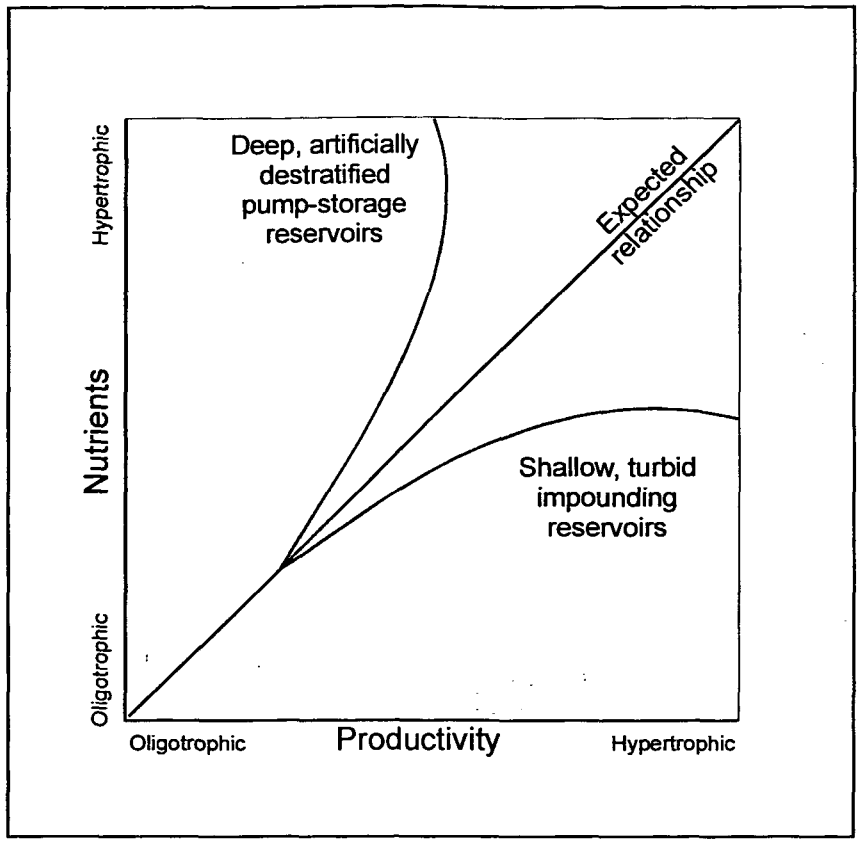


Figure 9.6 Deviations from expected nutrient / productivity relationships in UK lowland reservoirs. Trophic classifications for both nutrients (TP) and productivity (Chla / SD) are based on OECD (1982) criteria.

Stratification is important in the plankton ecology of deep natural lakes (Reynolds & Irish, 2000). Artificial destratification appears to reduce phytoplankton population growth in three ways. Firstly, it limits light availability to phytoplankton. Providing that the timing and intensity of mixing energy is appropriate for the reservoir concerned (Ridley, 1970), artificial destratification results in algal cells spending less time in the photic zone, leading to a decrease in phytoplankton biomass, well below the carrying capacity of the reservoir (Duncan, 1990; Brierley & Harper, 1999). This occurs because net algal growth represents a balance between photosynthesis and respiration, with photosynthesis limited to a water-body's upper layers (epilimnion), whilst respiration occurs throughout the water column. Vertical mixing stimulated by destratification reduces the ability of phytoplankton to congregate in the euphotic layer and photosynthesise. Thus where there is a large ratio of mixing depth to euphotic depth, respiration dominates algal metabolism and thus limits growth rates (Oskram & van Breemen, 1992).

Differences in hydraulic regimes as opposed to varying nutrient availability were described as being more influential in determining annual and interannual variability in the abundance

and composition of phytoplankton in 21 Sicilian reservoirs by Naselli-Flores (2000). Although none of the reservoirs was equipped with destratification equipment, the action of water abstraction (i.e. draw-down) in the summer months played a similar role, resulting in increased circulation and a deepening of the mixed layer (i.e. an increase in the mixing depth to euphotic depth), leading in turn to phytoplankton cells residing for longer periods in darkness. As a result, Naselli-Flores (2000) proposed that in the higher part of the trophic gradient, light availability provides the dominant influence on the species structure of the phytoplankton. This is similar to the pattern described for artificially destratified reservoirs and illustrates that a reduction in water level and subsequent deepening of the mixed layer creates a similar effect to artificial destratification. Drawdown also leads to the resuspension of particles into the water column and thus produces a similar effect to mixing, in that light availability is reduced.

In productivity experiments Brierley (1985) showed that mixing favoured phytoplankton species tolerant of a wide range of irradiances, describing this as a result of selection of species evolved to favour turbulent conditions or with the ability to regulate their own light climate by vertical movements. These populations also had lower assimilation rates compared to populations favouring stratified conditions. *Fragilaria crotonensis* is an example of a diatom taxon favoured by destratification. For example in Coldingham Loch, a small deep Scottish loch, Bailey-Watts (1986) showed that artificial mixing by aeration promoted the growth of *F. crotonensis*, which remained at very low numbers during the previous year when the loch stratified under natural conditions. Similarly Steinberg & Gruhl (1992) reported that artificial destratification in a small experimental lake in Bavaria changed the conditions for competition between phytoplankton species. Cyanophyte growth was disadvantaged whereas chlorophytes and diatoms, namely *F. crotonensis* gained an advantage. In the current study, seasonal phytoplankton data for the eutrophic, artificially destratified Chew Valley reservoir (see Chapter 6), illustrates that diatoms are the dominant component of the phytoplankton, with cyanophyte populations maintained at very low levels. *F. crotonensis* is the dominant diatom taxon, growing throughout the year except when nitrate, to which *F. crotonensis* has a low tolerance (Reynolds, 1984b), becomes limiting.

The second way in which artificial mixing limits algal productivity is through the impact of grazing by herbivorous zooplankton. In the man-made Biesbosch reservoirs (mean depths 13-15 m) in the Netherlands, Oskram and van Breeman (1992) noted that mixing over a sufficient depth retarded algal growth rate to levels where the zooplankton could 'keep up'

with the algae, suppressing them to low levels. Steinberg and Gruhl (1992) reported that in their whole-lake experiments in Fischkaltersee, a small Bavarian lake (mean depth 5.7 m, max. depth 11.2 m), zooplankton biomass, functionally dominated by the highly efficient cladoceran grazers actually increased after destratification. This was probably due to artificial destratification favouring chlorophytes and diatoms over the more filamentous cyanophytes, thus providing a more readily available and easily assimilated food source for zooplankton grazers. The establishment of a large population of efficient herbivorous zooplanktivores thus exerted an additional stabilising, top-down influence on the total phytoplankton community.

Finally, artificial destratification, where applied for intermittent periods, enables greater sedimentation of decaying phytoplankton biomass. In Fischkaltersee, a Bavarian lake, Steinberg and Gruhl (1992) demonstrated that a period of mixing was followed by a sudden cessation of movement if destratification equipment was switched off. During this period of quiescence, short periods of thermal and chemical stratification allowed sedimentation, which removed and thus reduced the algal populations present in the mixed layer when artificial mixing was restarted.

The factors discussed above appear to explain the divergence of deep, artifical pump storage reservoirs from the expected relationship between nutrient availability and productivity. By controlling the biomass of *r*-selected species (opportunists) e.g. many diatom taxa, and delaying the crop maxima of the K-selected (more efficient) 'summer species' e.g. most cyanophytes, the total standing crop of phytoplankton can be maintained below the nutrient-carrying capacity (Steinberg and Gruhl, 1992).

Higher productivity than expected from ambient nutrient concentrations

Sites with higher productivity levels than expected under relatively low nutrient concentrations comprise shallow, turbid, impounding reservoirs (Figure 9.6). Examples in the current study include Durleigh, Nanpantan, Powdermill, Sutton Bingham and Weir Wood. These reservoirs are generally shallow (mean depths of <5 m), turbid and lack extensive macrophyte growth. Shallow lakes are said to exist in two stable states (Scheffer, 1990; Moss *et al.*, 1996). One is the clear-water state, dominated by macrophytes, with phytoplankton growth increasing gradually with increasing nutrient availability, but kept in check by a combination of factors. These include competition from macrophytes, the effects of macrophytes securing sediments and thus preventing their resuspension and the high numbers of cladoceran zooplankton that graze phytoplankton and are protected from

predation by the presence of macrophytes. The alternative stable state is one with far higher productivity for the same nutrient concentration. In such systems macrophytes are absent, zooplankton are less abundant or absent and sediments are not protected by macrophyte cover. This state is referred to as the 'turbid' state. Scheffer (1990, p.479 - Figure 4) positions such turbid lakes much closer to the phytoplankton biomass axis, when plotted against nutrients, than deep lakes and shallow non-turbid lakes, which lie more centrally or closer to the nutrient axis.

There are several reasons why such turbid shallow lakes may appear more productive than their nutrient loads suggest. According to Moss *et al.* (1996), once a clear-water shallow lake has switched to a turbid state, negative feedback mechanisms maintain phytoplankton dominance even when nutrient levels are reduced. Paramount amongst these negative feedbacks is the absence of zooplankton, particularly cladocera. With no macrophytes for refuge, zooplankton are easy prey for zooplanktivorous fish. In deeper reservoirs, the hypolimnion may provide refuge for zooplankton since they can vertically migrate (Bronmark & Hansson, 1998) however such depth refuges are not available in shallower lakes. Thus in the absence of both macrophytes and vertical migration, zooplankton populations cannot be maintained. Most of the reservoirs mentioned support large populations of zooplanktivorous coarse fish species including roach (*Rutilus rutilus*) and bream (*Abramis brama*). In the absence of zooplankton, phytoplankton populations are not subjected to predation and can thus proliferate. In the current study, the reversal of this process was observed in Stanford reservoir (max depth 8.7m, mean depth 2.8m). Stanford experienced severe deoxygenation and a fish-kill following the death of a large bloom (1.5 million cells per litre) of the cyanophyte, *Oscillatoria* spp. in May 2000 (Mark Richardson, STW, pers. comm.). Before this catastrophic event, the water was turbid, with Chla concentrations of ~20 μgl^{-1} and SD ~1.0 m. After this event, the water became markedly clearer, with Chla concentrations of 2-4 μgl^{-1} and SD ~3.0 m. A clear-water state was maintained until the end of the sampling period. These observations support the results of biomanipulation studies in shallow lake ecosystems, where fish-removals are employed to facilitate the re-establishment of zooplankton populations and the return to a clear-water state (Søndergaard *et al.*, 1990; Moss *et al.*, 1996).

Another fish known to occur in several of these reservoirs is the common carp (*Cyprinus carpio*). Along with bream (*Abramis brama*), these species disturb lake sediments as they forage, uprooting and eating plants and mobilising phosphorus, thus providing phytoplankton with a steady source of available P, preventing limitation to phytoplankton

(Breukelaar *et al.*, 1994). A combination of sediment disturbance by benthivorous fish, heavy periphyton growth on developing plants and unstable sediment prevent the return of macrophytes, even when nutrient loads are reduced. Therefore once the turbid state is established the lack of zooplankton and the inability of macrophytes to recolonise results in the phytoplankton being unchecked by either competition or predation even when nutrient concentrations vary. Turbid states with high phytoplankton productivity are therefore able to exist over a considerable range of trophic conditions (Moss *et al.*, 1996). Nanpantan in this study (max depth 6.7 m, mean depth 4.1 m) provides a good example of a small, relatively shallow reservoir currently in a highly turbid but only moderately nutrient-rich state. It is stocked with benthivorous *C. carpio* L. and its limited littoral flora of *Myriophyllum spicatum* L. supports dense periphyton growth.

In summary, the relationship between nutrient availability and algal productivity can be weakened by two different mechanisms that are related to reservoir morphology. In deep artificially aerated reservoirs, algal productivity is lower than expected according to available nutrients, because destratification reduces the ability of phytoplankton to maximise their photosynthetic potential. In the shallower reservoirs in this study, the turbid alternative stable state is prevalent. Lack of macrophytes, leading to resuspension of sediments and the demise of zooplankton, enables phytoplankton to dominate unchecked in these systems, thus maximising their attainable biomass under available nutrient resources. This differing response of shallower and deeper UK lowland reservoirs has implications for the management of sites exhibiting differing morphologies.

9.3.2 Implications of the weak relationship between nutrients and productivity for reservoir management

In its wider sense eutrophication is important both in terms of cause (increased nutrient loading) and effect (increased phytoplankton productivity). In UK lowland reservoirs, nutrients and productivity do not co-vary as might be expected. Therefore to gain a more detailed portrayal of eutrophication in reservoirs both TP and Chla inference models should be applied.

With two main gradients influencing diatom distributions, it might seem appropriate to include together in inference model construction the two variables best representing the two axes of variation (TP and Chla in the current study). However, it is not considered meaningful to include two or more environmental variables in the same inference model (Korsman & Birks, 1996; Birks, 1998), despite clear evidence that multiple factors impact

upon species assemblages. Instead, the development and application of separate inference models for the reconstruction of both TP and Chla were found to be beneficial in the current study. Since some species show better responses to light availability than to nutrients and vice-versa, this helps to overcome the inadequacies of one or other reconstruction alone. For example, in the current study, *Fragilaria crotonensis* and *Asterionella formosa* show strong unimodal responses to Chla and SD but little or no response to TP. *Cyclotella radiosa* shows the inverse trend, whereas *Aulacoseira granulata* shows similar well-defined unimodal responses to both Chla and TP.

In the present study, the second axis of variation in the species - environmental dataset is dominated by the influence of Chla and SD. These variables are intrinsically linked to reservoir morphometry. SD, in particular, is determined to a large extent by the overall depth of the waterbody in which it is measured. A problem with environmental variables in calibration work arises when the variables of interest are largely "intrinsic morphometric features of each lake, for example water depth" (Birks, 1998, p.317). Environmental reconstructions using inference models assume a space-for-time substitution, however physical variables may be inappropriate for such substitution because they are, and have in the past been, constrained by the morphometry of the water body.

A further interesting feature of the second axis of variation in the UK lowland reservoirs dataset is that algal productivity (Chla) is associated with both reservoir morphometry (water depth and SD) and reservoir age. If reservoir age is intrinsically linked with reservoir design and in turn, algal productivity, then this raises questions about the usefulness of both Chla and TP in reservoir trophic classification and management. In the current study the older reservoirs are generally of the impounding type, set in shallow, natural catchments. Conversely the younger reservoirs are more manipulated systems, usually filled with water pumped from river systems lying beyond their natural catchments. As a result, younger reservoirs can be constructed with dimensions far greater than the volumes of water that their immediate natural catchments supply. Thus pump storage reservoirs possess characteristics more closely related to morphological features than to nutrients, which in turn are often further modified by active reservoir management strategies such as artificial destratification.

Since UK lowland reservoirs do not demonstrate a strong relationship between nutrient availability and algal productivity, it appears that they are more complicated systems than natural lakes in terms of their nutrient / productivity relations, with factors other than TP

(e.g. non-algal turbidities) affecting algal productivity (cf. Canfield & Bachmann, 1981). In the current study the dataset is limited to sites of one basic typology – UK lowland reservoirs. Inference model performance benefits from a calibration set composed of one main habitat – the plankton - and the inclusion of only sites meeting other prescriptive criteria (see Chapter 3). However, as previously discussed, even within a relatively small, typology-specific calibration set, considerable environmental variability still exists. The two distinct axes of variation in the UK lowland reservoirs calibration dataset may therefore support the development of individual shallow and deep reservoir calibration datasets. In the large, combined datasets (e.g. the EDDI Combined TP calibration set) both shallow and deep lakes are included. This helps to increase the range of the environmental variables sampled, but ignores the inherent differences in the responses of shallow and deep lakes to changes in nutrient concentrations. When a calibration set is composed of one main habitat e.g. the plankton, there is a clear correlation between species composition and changes in epilimnetic nutrient concentrations. When datasets include a mixture of plankton and periphyton and hence a diversity of habitats for diatom growth, the relationships between epilimnetic nutrient concentrations and species assemblages may become blurred and environmental reconstructions can yield spurious results (e.g. Bennion *et al.*, 2001; Sayer, 2001).

In natural lakes, Seip *et al.* (2000) suggest that if similar criteria for nutrient pollution loads are applied across regions with different lake types, the same end-point goals will be achieved in terms of Chla reduction and lake water transparency. However, as discussed in detail in Chapter 8, the superior relationship of Chla to reservoir morphology over nutrients is of potential relevance in terms of reservoir management. It raises concerns over the ability to manipulate *all* UK lowland reservoirs and their catchments to meet water quality targets via the implementation of traditional abatement measures such as nutrient reduction.

Whilst it is desirable to reduce nutrient loadings as a first step towards improvements in water quality (cf. Edmondson, 1991, Anderson & Rippey, 1994), further strategies should be employed, some of which will require tailoring to the specific idiosyncrasies of individual reservoirs. Generally, artificially aerated deeper reservoirs in the current study have lower than expected algal productivity in relation to nutrient availability. In such reservoirs artificial aeration acts positively, to reduce the effect of prolific algal blooms. This is not to say that destratification will eliminate algal blooms completely, merely that it can bring them under greater control than would be possible under naturally stratified conditions. Shallower reservoirs in the current study are generally turbid, exhibiting both

high algal productivity and resuspension of profundal sediments. Restoration of such sites to bring about an improvement in water quality and more efficient water treatment may be possible (Moss *et al.*, 1996). Costessey is a shallow reservoir that could be a model for this approach, since it has water with a high TP concentration, but lower than expected algal productivity and turbidity. This reservoir has a short water residence time (and thus rapid flushing and nutrient outflow) and supports prolific macrophyte growth, conditions that appear to overcome problems associated with high nutrient inflow waters and the consequent development of dense algal blooms.

9.4 Eutrophication and re-oligotrophication of UK lowland reservoirs

The application of inference models to two selected reservoirs, Blackbrook and Daventry, in this study, demonstrates the potential phases of the cultural eutrophication and re-oligotrophication of UK lowland reservoirs (Figure 9.7). This is not to say that the trends seen in other eutrophying or re-oligotrophying reservoirs will follow the same species shifts, or that the illustrated stages and their ordering will be followed exactly (See Chapters 2 and 8 for full details of eutrophication and re-oligotrophication processes). In the two reservoirs examined, five phases have been recognised.

Phase 1 ***Stabilising phase***

After its creation, Blackbrook reservoir followed an initial stage of development consisting of a period of ecosystem stabilisation. This appears to be equivalent to the sigmoidal phase in the ontogeny of natural lakes (Deevey, 1984). Species typical of this phase include *Diatoma tenuis* var. *elongatum*, a taxon commonly reported in other newly filled reservoirs and during periods of nutrient enrichment (Atkinson, 1988; Holz et al., 1997, Leitão & Léglize, 2000).

Phase 2 ***Mesotrophic phase***

Following the stabilisation phase, and prior to any anthropogenic perturbations, Blackbrook reservoir experienced a period of relatively stable mesotrophy. This is equivalent to the equilibrium phase seen in the development of natural lakes. Species typical of this phase include *Aulacoseira subarctica*, *Cyclotella radiosa* and *Fragilaria crotonensis*. These taxa are often reported to be abundant in mesotrophic natural lakes (e.g. Canter & Haworth, 1991).

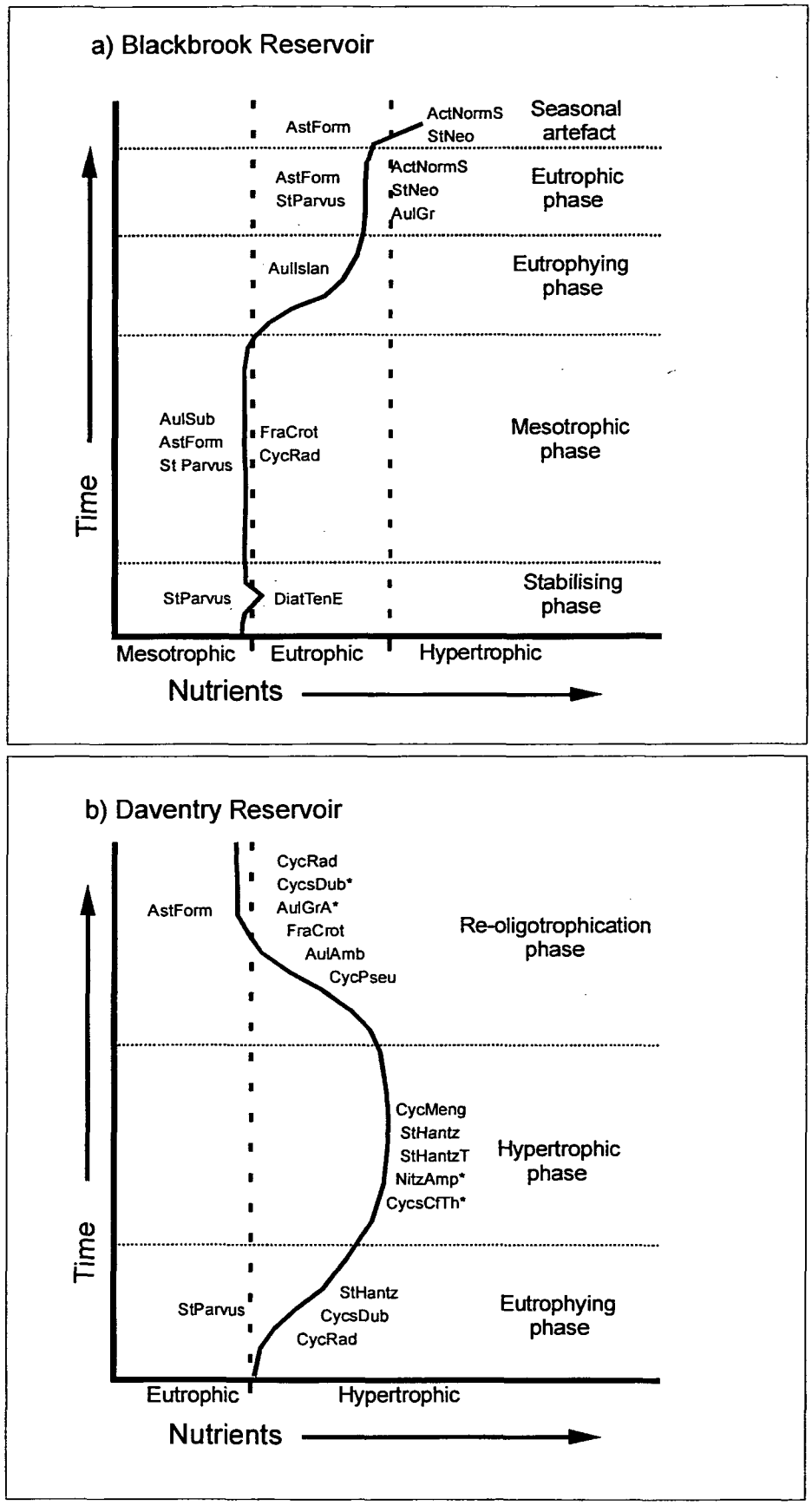


Figure 9.7 **Reconstructions showing eutrophication and re-oligotrophication at a) Blackbrook and b) Daventry reservoirs. Species on the left of the reconstruction line are spring-blooming species, those on the right are summer-blooming and those with an asterisk show no clear seasonal preference (Chapter 6 details seasonal preferences from this study).**

Phase 3 ***Eutrophying phase***

Subsequent to the stable mesotrophic phase, Blackbrook reservoir experienced cultural enrichment apparently from diffuse sources. This phase is equivalent to the displacement phase of Deevey (1984). At the outset of eutrophication, *Aulacoseira islandica* increased in relative abundance and overall diatom productivity increased markedly (cf. Willén, 1992; Reynolds & Irish, 2000; Liukkonen *et al.*, 1993). As eutrophication progressed, conditions favoured the dominance of *Stephanodiscus neoastraea*, *Actinocyclus normanii* fo. *subsalsa* and *Aulacoseira granulata* (cf. Stoermer *et al.*, 1987b; Lotter, 1998).

Phase 4 ***Hypereutrophic phase***

As cultural eutrophication continues unabated and nutrient supplies remain constant or increase, reservoir trophic state can increase from eutrophic to hypertrophic. This coincides with the period of indirect sewage pollution to Daventry reservoir. Species typical during this hypertrophic phase include *Stephanodiscus hantzschii* (and fo. *tenuis*), *Cyclotella meneghiniana*, *Cyclostephanos* cf. *tholiformis* and *Nitzschia amphibia*. These taxa are typical of both hypertrophic lowland rivers, reservoirs and natural lakes (e.g. Fritz, 1989; Lotter, 1989; Anderson, 1990a; Kiss *et al.*, 1990; Edmondson, 1991; Bennion, 1994, 1995; Tibby, 2004).

Phase 5 ***Re-oligotrophication phase***

Following elimination of the point source of pollution to Daventry reservoir, nutrient concentrations decreased and the reservoir recovered from a hypertrophic to a eutrophic state. The diatom species occurring in this phase include many of those that were present prior to the period of hypertrophy e.g. *Cyclotella radiosa*, *Cyclostephanos dubius* and *Cyclotella pseudostelligera*. Species new to Daventry's sedimentary record following re-oligotrophication include *Aulacoseira ambigua* and *Fragilaria crotonensis*. Since Daventry's sedimentary record does not extend back in time to its inauguration as a reservoir, it is not known whether the current assemblage comprises both returning and new taxa, or whether the 'new' taxa were actually present at some point in Daventry's early history. However the overall re-oligotrophication trend in species assemblage is broadly similar to that reported by Wessels *et al.* (1999) for Lake Constance, Germany.

Although hysteresis (lagging of effect behind cause) may be expected, the phytoplankton appears to respond relatively rapidly to changes in nutrient availability (cf. Anderson *et al.*, 1990; Anderson & Rippey, 1994). Although there may also be stochastic changes in phytoplankton populations both intra- and inter-annually, the smoothing effect of the sediment record incorporates this temporal variability and coarse resolution studies would appear to be sufficient for the assessment of perturbations occurring during the relatively short histories of individual reservoir ecosystems (Tibby, 2004).

The results of the current study support the view of Reynolds (1999) that in both natural lakes and reservoirs, the selective mechanisms determining phytoplankton populations are similar, but the selective outcomes are very much influenced by environmental conditions and the type of management applied. In common with the results of studies from shallow lakes (e.g. Lake Trummen discussed in Moss *et al.*, 1996), de-stabilising 'catastrophic' events appear necessary to provide a switching mechanism between turbid and clear-water states in the shallowest UK lowland reservoirs. In contrast, deeper reservoirs show re-oligotrophication characteristics similar to those seen in deeper natural systems, where nutrient concentrations are more intimately linked with phytoplankton population dynamics. A simple reduction in nutrient availability would appear to be sufficient to bring about a relatively rapid shift in phytoplankton composition and biomass in Daventry reservoir (see discussion in section 8.4.5). Therefore measures such as sewage diversion and the reduction of diffuse nutrient inputs from agriculture also have the potential to bring about a similarly rapid recovery from nutrient-related perturbations in other deep UK lowland reservoirs.

9.5 Summary Points

- During the development and application of diatom-based inference models, numerous decisions must be made – many subjective – that impact directly upon the ultimate interpretive value of environmental reconstructions.
- The environmental variables reconstructed in this study independently explain a maximum of 6% of the variance in the diatom species data. Thus reconstruction of a single environmental variable cannot account for the multitude of factors influencing the composition of diatom species assemblages.
- Taphonomic processes, such as dissolution, breakage and the seasonality of individual diatom species, influence the transition of 'live' diatom populations to fossil assemblages. Adapted surface sediment sampling methodologies can be employed to reduce the impact of these processes, however, taphonomy cannot be

eliminated and thus its influence must be understood and accounted for in palaeolimnological studies of individual reservoirs.

- The accurate definition of species optima is vital for the creation of effective diatom-based WA inference models. However, optima assigned to individual species are dependant upon the length of the environmental gradient in the calibration dataset and may also be affected by the heterogeneity of habitats in calibration set sites. Definition of optima may be improved through selection of calibration set sites spanning longer environmental gradients, by carefully amalgamating regional calibration datasets or by developing habitat-specific calibration datasets. Alternatively, those species that show no clear response to the variable under reconstruction could be eliminated from the calibration set to improve model performance, or other modelling methods, such as ANNs, could be applied alongside WA models to enable comparison of reconstructed values.
- In the UK lowland reservoir dataset, there is considerable variation in the composition of diatom assemblages between sites at the lower end of the TP gradient (<32 μgl^{-1} TP). Above ~135 μgl^{-1} TP, any further increase in TP concentration appears to result in very little change in the species composition of diatom assemblages. This may be because other factors such as hydraulic regimes are having a greater influence on species composition at these high TP levels. In such sites, reconstruction of other variables may be of greater value. Alternatively the use of other environmental indicators that may respond to changes in TP above 135 μgl^{-1} should be considered.
- Planktonic diatoms dominate UK lowland reservoirs. The performance statistics of the plankton-only models developed in this study were only slightly less strong than those including all taxa. Identification of the smaller range of planktonic diatom taxa, as opposed to identifying taxa from all habitats, may make the utilisation of such diatom-based inference models more accessible to those, such as Water Companies, who may consider their adoption for reservoir management purposes.
- Within the UK lowland reservoir calibration dataset, there appear to be two axes of variation. The first is related to nutrient availability and ionic concentrations, and the second reflects an algal productivity gradient. This appears to contrast with the expected close relationship between nutrient availability and algal productivity. Sites with lower productivity than expected for their ambient nutrient concentrations are deep, artificially destratified, pumped-storage reservoirs. Sites with higher than expected productivity in relation to available nutrients, are shallow, turbid

reservoirs, where phytoplankton is able to dominate in the absence of zooplankton grazers or competition from macrophytes.

- The presence of two axes of variation must be accounted for when reconstructing reservoir nutrient histories using diatom-based inference models. The application of both TP and Chla reconstructions to reservoirs may yield a fuller account of a reservoir's history than could either model alone. Management and restoration of reservoirs must also take account of the indirect relationship between nutrients and productivity. Dependant on individual reservoir characteristics, bespoke restoration strategies may need to be devised and employed.
- Application of diatom-based TP, Chla and EC inference models to two selected reservoirs in this study highlight many of the key phases of development that reservoirs in the UK may experience. They show that whilst eutrophication of UK lowland reservoirs continues to occur, for example at Blackbrook reservoir, positive management strategies and the use of remedial measures, such as those employed at Daventry reservoir, can result in a rapid recovery (i.e. re-oligotrophication) of reservoir ecosystems.

CHAPTER TEN

Conclusions and future work

10.1 Introduction

This chapter provides a summary of the results and discourse generated by this thesis. It is divided into three parts. The first briefly restates the original aims of the study. The second presents the main conclusions drawn from the thesis and is divided into three parts, reservoir environments and diatom ecology, transfer function development and application and reconstructing past environments in UK lowland reservoirs. Finally, potential directions for future work are examined with reference to the main issues raised over the course of this study.

10.2 Original aims

The original aim of this study was to investigate the potential of UK lowland reservoirs for the development of diatom nutrient palaeolimnological inference models by:

1. creating a calibration dataset for UK lowland reservoirs spanning a broad trophic gradient, comprising mean annual environmental data and surface sediment diatom assemblages.
2. developing diatom-inference models for the reconstruction of eutrophication histories and comparing the performance of plankton-only models with those based on all taxa.
3. applying these models to down-core changes in sedimentary diatom assemblages for selected reservoirs, and comparing diatom-inferred trajectories with historic records.
4. investigating the seasonality displayed by reservoir planktonic diatom assemblages in response to environmental conditions and exploring relationships between live and fossil diatom assemblages to aid interpretation of sedimentary diatom records.

10.3 Reservoir environments and diatom ecology

- The water column provides the dominant habitat for diatom growth in UK lowland reservoirs. Consequently, planktonic diatom taxa dominate the surface sediment diatom assemblages of these sites (~70% mean relative abundance). This helps to explain the close similarities in statistical performance and predictive capabilities of the plankton-only model and that based on all taxa. It is not thought that the development of models specific to other habitats i.e. those based solely on epiphytic,

epilithic or epipelic taxa would be prudent as it is expected that they would yield lower performance statistics because of the relative insignificance of these habitats for diatom growth in UK lowland reservoirs.

- Many diatom taxa display defined seasonal growth preferences. Dissolved silica (Si), secchi depth (SD), conductivity (EC) and pH were found to be the most influential environmental variables in determining the seasonality of planktonic diatom taxa in nine selected reservoirs. Seasonal variation in Si concentrations and availability in relation to phosphorus and nitrogen concentrations, are more important in explaining *seasonal* shifts in planktonic diatom assemblages than in determining *mean annual* surface sediment diatom assemblages.
- In reservoirs displaying high levels of productivity and thus high sedimentation rates, the 0-0.5 cm depth sample may be a seasonal artefact, dominated by diatom taxa that occurred at a high percentage relative abundance in the reservoir plankton in the period prior to sediment sampling. In reservoirs with moderate to high sedimentation rates, the 0.5-1 cm depth sample may provide the best representation of diatom plankton populations present in the reservoir during the year prior to sediment sampling. In reservoirs with a low sedimentation rate, the 0-0.5 cm depth sample may be more representative of the same period. However where the sedimentation rate is unknown a well-homogenised 0-1 cm depth sample may provide the best compromise.
- In UK lowland reservoirs, it appears that the response of diatom assemblages to total phosphorus (TP) shows little change above concentrations of 100-150 μgl^{-1}. It is possible that phosphorus is no longer the limiting nutrient at these high concentrations and that other factors such as turbulence from artificial destratification may become more important in determining species distributions. This could also indicate that fewer taxa are ecologically adapted to tolerate high TP concentrations and consequently other algal groups may be advantaged. Alternatively, when TP concentrations are high, there may be fewer ecological niches available and thus a restricted range of diatom taxa can coexist.

10.4 Transfer function creation and application

- UK lowland reservoirs are suitable sites for the development of statistically robust transfer functions for the reconstruction of TP, chlorophyll-*a* (Chla) and conductivity (EC). Development of transfer functions for UK lowland reservoirs extends the range of lake typologies for which diatom-based inference models have been created. These models can be used as they were designed specifically for the

purpose of reconstructing individual reservoir trophic histories. Potential also exists for incorporation of the current study's calibration set into merged datasets and combined models (e.g. the EDDI Combined TP model) to increase their performance across a wider range of lake typologies. However it has been noted that caution must be taken when combining datasets and applying such composite models.

- There are a number of issues relating to the development and application of diatom-based inference models that should be taken into account when drawing conclusions from reconstructed values. In this study, no individual environmental variable was shown to explain >7.1% conditional variance and >5.7% marginal variance in the diatom species data. Therefore the overall value of reconstructing single environmental variables from diatom assemblages is questionable when multiple factors are known to influence species distributions. In addition, weighted averaging (WA) optima show considerable variability between published datasets. Many of the taxa in this study showed no clear response to the variables for which inference models were created and as a result their optima may be poorly defined and should not be relied upon to reconstruct 'absolute' values. For each individual published dataset, the defined species' optima largely reflect the length of the calibration set's environmental gradient and are thus relative within, but not between datasets. Combining datasets may therefore generate spurious results since wide-ranging optima defined under different regional models for each taxon merely produce 'mean' values bearing little ecological relevance. It is therefore perhaps more appropriate to take a semi-quantitative approach by considering the shift in overall species' assemblages as opposed to relying on individual species optima to indicate changes in trophic status. The use of 'target' diatom assemblages (i.e. an extension of Reynold's (1984b) approach) may provide a more ecologically meaningful means of determining trophic state as opposed to simply defining non-universally applicable optimal values.

10.5 Reconstructing palaeo-environments in UK lowland reservoirs

- Diatom-inferred reconstructions for Blackbrook and Daventry reservoirs indicate that the models developed in this study are capable of recognising both increases (eutrophication) and decreases (re-oligotrophication) in trophic status, which are supported by historical records. The transfer functions created in this study are therefore of potential benefit for the management of reservoirs, both in terms of enabling assessment of past perturbations and recoveries, and in the setting of future

restoration targets and development of management strategies. As demonstrated for Daventry reservoir, there is an argument for reconstructing more than one environmental variable, especially where analysis of the calibration dataset highlights more than one strong axis of variation in the diatom species data and/or where reconstructed trajectories for one variable produce spurious results.

- Although fossil diatom dissolution was not a problem in the sedimentary records of either Blackbrook or Daventry reservoirs, this is not the case for many other UK lowland reservoirs. Thus despite the predictive capabilities of the models created in the current study, there may be few lowland reservoir sites in the UK that possess undissolved diatom records at which the models can be applied. In addition, many reservoirs, particularly older sites, have undergone sediment removal at some stage in their history to restore maximal water storage capacity. Dredging may mean that palaeolimnological techniques are unable to capture a reservoir's complete history and thus cannot lead to the establishment of non-impacted base-line conditions for the subsequent implementation of restoration targets. However, as seen for Daventry reservoir, sedimentary diatom remains and associated diatom-inferred reconstructions can provide useful information relating to reservoir history irrespective of the temporal extent of the sedimentary record. Thus dredging does not invalidate use of palaeolimnological inference model techniques over the short sedimentary sequences often found in reservoirs, provided that the recently accumulated sediment stratigraphy is undisturbed. Additionally, since diatom species assemblages in both natural and artificial waterbodies are very similar, it is envisaged that the models created in the current study could also be applied to diatom records from non-reservoir sites supporting similar species and environmental characteristics to those included in the UK lowland reservoirs calibration set.
- There are two main axes of variation in the calibration dataset. The first is a water chemistry gradient related to both nutrients and ionic concentration. The second is related to algal productivity and reservoir morphology. In contrast with published trends for natural lakes, the relationship between nutrient concentrations and algal productivity is only very weak in UK lowland reservoirs. This may be attributed to the occurrence of non-algal turbidities in the shallower impounding reservoirs and the influence of artificial destratification in the deeper pump-storage sites. These effects appear to breakdown the relationship between available nutrient concentrations and resultant algal productivity. For example, many shallow turbid reservoirs have higher algal productivity than predicted from available nutrient

concentrations, whereas many deeper, destratified pump-storage reservoirs have lower algal productivity than predicted. Physical factors relating to reservoir morphology e.g. water depth, and management techniques such as destratification, may therefore be just as important as chemical conditions in determining trophic status in UK lowland reservoirs. If nutrients and productivity are not intimately related in many reservoirs, this raises issues concerning the applicability of simple criteria based on water chemistry e.g. OECD (1982) for the classification of reservoir trophic state.

10.6 Future work

- Analyses of seasonal plankton samples from additional reservoirs should help to improve definition of the seasonal preferences of individual planktonic diatom taxa and aid clarification of seasonal trajectories shown by diatom species assemblages in UK lowland reservoirs. To determine the environmental optima and tolerances of individual diatom taxa in relation to trophic variables, if any such absolute values actually exist, it may also be informative to pursue a controlled experimental approach (ideally field-based). This may better aid interpretation of stratigraphic diatom records, perhaps shedding greater light on competitive interactions between different planktonic diatom species and other algal groups.
- Increasing the length of the TP gradient may improve the definition of optima for some taxa currently displaying truncated distribution curves in the calibration dataset. It is unlikely however that many further suitable lowland reservoir sites exist in the UK, particularly at the low end of the TP gradient where pH and factors relating to habitat heterogeneity appear to confound diatom-nutrient relationships. It is therefore suggested that the calibration set of UK lowland reservoirs could be amalgamated with similar regional datasets dominated by moderate to deep-water lakes, to create a large combined dataset. This could then be applied directly to sediment cores for reconstruction, or alternatively, prior to model application, the merged dataset could be subjected to modern analogue technique (MAT) analysis for selection of a range of modern samples most similar to each of the fossil samples. This would form a bespoke training set specific to the fossil sequence under reconstruction, which could potentially improve the predictive ability of model inferences. Alternatively shorter sections of the overall longer environmental gradient could be analysed using linear-based statistical techniques e.g. partial least squares (PLS). It may also be fruitful to remove diatom taxa that show little response to changes in the environmental variable under reconstruction and focus

concentration instead on those taxa demonstrating a clear response. This would remove the influence of poorly defined optima on model-reconstructed values and thus should lead to improvements in inference model performance statistics. Artificial Neural Networks (ANNs) could be applied alongside the traditional Weighted Averaging (WA) approach to cross-validate model inferences. A further alternative approach might involve amalgamating typology-specific datasets from other world regions to create a reservoir-specific calibration dataset and inference models. This would have the advantage of increasing the length of the environmental gradients in the calibration dataset, whilst also limiting lake typology to one particular type – reservoirs, thus reducing problems associated with both habitat heterogeneity and harmonisation between datasets.

- Poor preservation of fossil diatom assemblages, in particular diatom dissolution, is of particular relevance when attempting to apply diatom-based inference models to sedimentary sequences from UK lowland reservoirs. It may therefore be beneficial to investigate the potential of utilising other organism groups (e.g. chironomids or testate amoebae) or biological indicators (e.g. algal pigments) in place of diatoms. It may also be informative to analyse in tandem, groups from different trophic levels and thus take a multi-proxy approach to reconstructing reservoir trophic histories.

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Appendices

APPENDIX ONE

List of abbreviations used in this study

Abbreviation	Full name / description
Age	Age of reservoir (years)
Alk	Alkalinity (mgl^{-1})
Alt	Altitude of reservoir (metres above Ordnance Datum (m.a.O.D.))
Ca / Ca^{2+}	Calcium ion concentration (mgl^{-1})
Cat	Catchment area of reservoir (km^2)
Chla / Chl-*a*	Chlorophyll-*a* concentration (annual mean concentration) (μgl^{-1})
ChlaM	Chlorophyll-*a* concentration (annual maximum concentration) (μgl^{-1})
Cl / Cl^-	Chloride ion concentration (mgl^{-1})
(p)CCA	(partial) Canonical Correspondence Analysis
DCA	Detrended Correspondence Analysis
Destrat	Destratification of the reservoir (yes / no)
EC	Electrical Conductivity (μScm^{-1})
Geol	Predominant catchment geology (1, acidic: 2, neutral: 3, alkaline)
K / K^+	Potassium ion concentration (mgl^{-1})
Z_{max}	Maximum water depth (m)
Z_{mean}	Mean water depth (m)
Mg / Mg^{2+}	Magnesium ion concentration (mgl^{-1})
Na / Na^+	Sodium ion concentration (mgl^{-1})
PCA	Principal Components Analysis
pH	pH of water
Res Time	Residence time of water in the reservoir (days)
SD	Secchi Depth (cm)
Si / SiO_2-Si	Dissolved Silica concentration (mgl^{-1})
SRP	Soluble Reactive Phosphorus concentration (μgl^{-1})
TN	Total Nitrogen concentration (mgl^{-1})
TON / NO_3-N	Total Oxidised Nitrogen concentration (mgl^{-1})
TP	Total Phosphorus concentration (μgl^{-1})
Type	Reservoir type (1, spring-fed: 2, impounding: 3, mixed impounding and pumped storage: 4, pumped storage)
Vol	Reservoir capacity (Ml)
(%)Agri	Percentage of agricultural land in the reservoir catchment (%)
(%)Conif	Percentage of coniferous forest in the reservoir catchment (%)
(%)Decid	Percentage of deciduous woodland in the reservoir catchment (%)
(%)Res	Reservoir surface area as a percentage of the reservoir catchment (%)
(%)Urban	Percentage of urban land in the reservoir catchment (%)
AW	Anglian Water
BWW	Bristol Water Works
BWB	British Waterways Board
CDW	Corby & District Water Company
SESW	Sutton & East Surrey Water
SEW	South East Water
SWW	South West Water
WW	Wessex Water

APPENDIX TWO

Calibration dataset sites, numbers, codes & surface sediment samples

Reservoir	No.	Code	Date recovered	Water depth (m)	Surface sediment colour / description and notes
Ardleigh	1	ARD	29/09/00	11.4	0-2 cm: 2.5Y 3/3 dark olive brown
Blackbrook	2	BBK	25/09/00	11.3	0-0.5 cm: 10YR 2/2 very dark brown (unconsolidated sediment with chironomid casts on surface), 0.5-2 cm:10YR 3/2 very dark grayish brown
Blagdon	3	BLG	07/10/00	7.7	0-0.5 cm: 10YR 3/3 dark brown (much organic matter and chironomid casts, 0.5-2 cm: 10YR 4/3
Blithfield	4	BLI	23/09/00	12.6	0-2 cm: 7.5YR 3/3 dark brown. Lots of *Anabaena flos aqua* strands on sediment surface. (0-0.5 cm unconsolidated / smelly).
Cheddar	5	CHD	07/10/00	7.5	0-2 cm: 10YR 3/3 dark brown. *Ceratophyllum demersum* and *Chara* spp. remains and live plants growing on sediment surface.
Chelmarsh	6	CHL	23/09/00	16.3	0-2 cm: 10YR 3/4 dark yellowish brown
Chew Valley	7	CHW	07/10/00	6.0	0-2 cm: 7.5YR 3/3 dark brown (chironomid casts)
Clatworthy	8	CLA	21/10/00	21.7	0-1 cm: 10YR 3/3 dark brown (black below)
Costessey	9	COS	29/09/00	3.4	0-2 cm: 2.5Y 3/3dark olive brown (some chironomid casts)
Cropston	10	CRO	25/09/00	5.0	0-2 cm: 10YR 2/2 very dark brown
Draycote	11	DRA	26/09/00	8.2	0-2 cm: 2.5Y 4/3 olive brown
Durleigh	12	DUR	08/10/00	4.0	0-2 cm: 7.5YR 3/4 dark brown
Eyebrook	13	EYE	28/09/00	8.5	0-2 cm: 2.5Y 4/4 olive brown
Foremark	14	FOR	24/09/00	19.8	0-2 cm: 7.5YR 3/3 mid-brown
Foxcote	15	FOX	27/09/00	4.7	0-2 cm: 2.5Y 4/4 olive brown
Grafham	16	GRF	28/09/00	13.0	0-2 cm: 5Y 4/4 olive (undecayed algal remains in top 1.5cm)
Hawkridge	17	HAW	08/10/00	9.1	0-2 cm: 7.5YR 3/3 dark brown
Hollowell	18	HOL	27/09/00	6.0	0-2 cm: 2.5Y 3/3 dark olive brown
Leigh	19	LEI	08/10/00	9.2	0-2 cm: 10YR 3/3 dark brown (flocculent and organic with chironomids). Many *Chaoborus* spp. in water
Luxhay	20	LUX	08/10/00	8.8	0-2 cm: 10YR 3/3 dark brown (FLAB rising from sediment surface and chironomids in sediment)
Nanpantan	21	NAN	25/09/00	4.8	0-2 cm: 10YR 3/3 dark brown
Ogston	22	OGS	24/09/00	9.1	0-2 cm: 2.5Y 4/3 olive brown (1-2 cm; iron oxides and black organics
Pitsford	23	PIT	27/09/00	11.6	0-2 cm: 2.5Y 4/4 olive brown
Porth	24	POR	28/10/00	7.5	0-2 cm: 2.5Y 3/3 dark olive brown (with organics)
Ravensthorpe	25	RAV	27/09/00	7.0	0-1 cm: 10YR 3/3 dark brown, 1-2 cm: 2.5Y 3/3 dark olive brown
Rutland	26	RUT	28/09/00	21.2	0-2 cm: 2.5Y 4/4 olive brown
Stanford	27	STF	26/09/00	3.8	0-2 cm: 2.5Y 4/3 olive brown
Staunton Harold	28	STN	24/09/00	16.9	0-2 cm: 2.5Y 3/3 dark olive brown
Stithians	29	STI	16/06/00	12.2	0-2 cm: 10YR 2/2 very dark brown (flocculent and organic)
Sutton Bingham	30	SUT	14/06/00	8.0	0-2 cm: 5Y 5/4 olive
Swithland	31	SWI	25/09/00	4.5	0-0.5 cm: 10YR 3/3 dark brown, 0.5-2 cm: 10YR 3/2 very dark grayish brown
Thornton	32	THO	26/09/00	6.6	0-2 cm: 10YR 3/4 dark yellowish brown
Tittesworth	33	TIT	23/09/00	11.2	0-2 cm: 2.5YR 3/3 dark olive brown (chironomid casts on surface)
Trenchford	34	TRE	19/10/00	10.0	0-2 cm: 10YR 2/2
Trimpley	35	TRI	23/09/00	9.3	0-2 cm: 10YR 3/4 dark yellowish brown
Upper Tamar	36	UPT	16/06/00	9.1	0-2 cm: 2.5Y 3/3 dark olive brown
Wimbleball	37	WIM	21/10/00	23.8	0-2 cm: 7.5YR 2.5/2 very dark brown (some chironomid casts)
Wistlandpound	38	WIS	19/10/00	21.6	0-2 cm: 10YR 2/2 very dark brown (flocculent and organic)
Ardingly	39	ARG	30/09/00	7.1	0-2 cm: 10YR 3/4 dark yellowish brown
Arlington	40	ARL	01/10/00	6.0	0-2 cm: 2.5Y 4/4 olive brown
Bewl	41	BEW	01/10/00	18.0	0-0.5 cm: 10YR 3/3 dark brown (some chironomid casts), 0.5-1 cm: 2.5YR 3/3 dark olive brown, 1-2 cm: 2.5Y 2.5/1 black
Bough Beech	42	BOU	30/09/00	14.9	0-2 cm: 2.5Y 5/4 light olive brown
Darwell	43	DAR	01/10/00	8.5	0-0.5 cm: 2.5Y 4/4 olive brown, 0.5-2 cm: 2.5Y 3/2 very dark grayish brown
Powdermill	44	POW	01/10/00	5.0	0-1 cm: 10YR 2/2 very dark brown (chironomid casts), 1-2 cm: 10YR 3/4 dark yellowish brown
Weir Wood	45	WEI	30/09/00	6.9	0-2 cm: 2.5Y 3/3 dark olive brown (gritty)
Daventry	46	DAV	26/09/00	5.3	0-2 cm: 2.5Y 3/3 dark olive brown (iron oxides)

APPENDIX THREE

List of abbreviations used for species in tables and diagrams

Abbreviations for the 94 dominant diatom species (present in a minimum of two reservoirs and occurring at ≥1% relative abundance in at least one site) referred to in text and diagrams

* Denotes the 39 'planktonic' / 'tychoplanktonic' species referred to in the plankton-only dataset. Those species which are shaded and listed at the end of the table are 'planktonic' but do not meet the criteria for inclusion in the plankton-only dataset.

Taxon code	Full taxon name and authority
AchLan	*Achnanthes lanceolata* (Breb. ex Kutz.) Grun. in Cleve & Grun., 1880
AchMin	*Achnanthes minutissima* Kutz. 1833
AchOblo	*Achnanthes oblongella* Ostr. 1902
ActNorm*	*Actinocyclus normanii* fo. *subsalsa* (Juhl.-Dannf.) Hust. ex VanLand. 1967
AmphInar	*Amphora inariensis* Krammer
AmphLib	*Amphora libyca* Ehrenb. ex Kutz. 1844
AmphPed	*Amphora pediculus* (Kutz.) Grun. ex A. Schmidt 1875
AnomVit	*Anomoeoneis vitrea* (Grun.) R. Ross in Patr. & Reimer 1966
AstForm*	*Asterionella formosa* Hassall 1850
AulAmb*	*Aulacoseira ambigua* (Grun. in Van Heurck) Simonsen 1979
AulGr*	*Aulacoseira granulata* (Ehrenb.) Simonsen 1979
AulGrA*	*Aulacoseira granulata* var. *angustissima* (O.Müll.) Simonsen 1979
AulGrACu*	*Aulacoseira granulata* var. *angustissima* fo. *curvata*
AulIslan*	*Aulacoseira islandica* (O.Müll) Simonsen 1979
AulSub*	*Aulacoseira subarctica* (O.Müll) Haworth
AulSubB*	*Aulacoseira subarctica* fo. *subborealis* (O.Müll) Haworth
CocPed	*Cocconeis pediculus* Ehrenb. 1838
CocPlac	*Cocconeis placentula* Ehrenb. 1838
CycsDub*	*Cyclostephanos dubius* (Fricke in A.Schmidt) Round 1982
CycsInv*	*Cyclostephanos invisitatus* (Hohn & Hellerman) Stoermer, Håkansson & Theriot comb. nov. 1987
CycsCfTh*	*Cyclostephanos* cf. *tholiformis* Stoermer, Håkansson & Theriot 1987
CycAtm*	*Cyclotella atomus* Hust. 1937
CycMeng*	*Cyclotella meneghiniana* Kütz. 1844
CycOcel*	*Cyclotella ocellata* Pant. 1902
CycPseu*	*Cyclotella pseudostelligera* Hust. 1939
CycRad*	*Cyclotella radiosa* (Grun.) Lemmermann & Håkansson 1988
CymMic	*Cymbella microcephala* Grun. in Van Heurck 1880
CymSin	*Cymbella sinuata* Greg. 1856
DentKuet	*Denticula kuetzingii* Grun.
DiatTenE*	*Diatoma tenuis* var. *elongatum* Lyngb. 1819
DiatVul*	*Diatoma vulgaris* Bory 1824
DipPar	*Diploneis parma* Cleve 1891
EncyCaes	*Encyonema caespitosum* Kutz. 1849
EncyGra	*Encyonema gracile* Ehrenberg 1841
EncySil	*Encyonema silesiacum* (Bleisch in Rabenhorst) Mann 1990
EunMin	*Eunotia minor* (Kutz) Grunow in Van Heurck 1881
FraBrev	*Fragilaria brevistriata* Grun. in Van Heurck 1885 *Pseudostaurosira brevistriata* (Grun. in Van Heurck) Williams & Round 1987
FraCapM*	*Fragilaria capucina* var. *mesolepta* (Rabenh.) Rabenh. 1864
FraConB	*Fragilaria construens* fo. *binodis* (Ehrenb.) Grun. 1862
FraConC	*Fragilaria construens* (Ehrenb.) Grun.1862 *Staurosira construens* (Ehrenb.) 1843
FraConV	*Fragilaria construens* var. *venter* (Ehrenb.) Grun. in Van Heurck 1881

Taxon code	Full taxon name and authority
FraCrot*	*Fragilaria crotonensis* Kitton 1869
FraEllip	*Fragilaria elliptica* Schumann 1867
	Staurosirella elliptica (Schumann) Williams & Round 1987
FraPinn	*Fragilaria pinnata* Ehrenb. 1843
	Staurosirella pinnata (Ehrenb.) Williams & Round 1987
FraVau	*Fragilaria vaucheriae* (Kutz.) J.B. Petersen 1938
FraVir	*Fragilaria virescens* Ralfs 1843
GomAng	*Gomphonema angustatum* (Kutz.) Rabenh. 1864
GomMint	*Gomphonema minutum* (Ag.) Ag. 1831
GomPar	*Gomphonema parvulum* (Kutz.) Kutz. 1849
GomPsT	*Gomphonema pseudotenellum* Lange Bertalot 1985
GomPum	*Gomphonema pumilum* (Grun.) Reichardt & L-B
GomOli	*Gomphonema olivaceum* (Hornemann) Breb. 1838
GomOliM	*Gomphonema olivaceum* var. *minutissimum* Hust.
GyroAcc	*Gyrosigma acuminatum* (Kutz.) Rabenh. 1853
MelVar*	*Melosira varians* Ag. 1827
NavCap	*Navicula capitata* Ehrenb. 1838
NavCapr	*Navicula capitatoradiata* Germain 1981
NavCari	*Navicula cari* Ehrenb. 1836
NavCrypt	*Navicula cryptocephala* Kutz. 1844
NavExil	*Navicula exilis* Kutz. 1844
NavGreg	*Navicula gregaria* Donk. 1861
NavLan	*Navicula lanceolata* (Ag.) Ehrenb. 1838
NavLep	*Navicula leptostriata* Jorgensen 1948
NavMen	*Navicula menisculus* Schum. 1867
NavPslan	*Navicula pseudolanceolata* Lange-Bertalot 1980
NavPup	*Navicula pupula* Kutz. 1844
NavRad	*Navicula radiosa* Kutz. 1844
NavTri	*Navicula tripunctata* (O.F. Mull.) Bory 1822
NavVen	*Navicula veneta* Kutz. 1844
NitzAmp	*Nitzschia amphibia* Grun. 1862
NitzDis	*Nitzschia dissipata* (Kutz.) Grun. 1862
NitzFont*	*Nitzschia fonticola* Grun. in van Heurck 1881
NitzGrac*	*Nitzschia gracilis* Hantzsch. 1860
NitzPal*	*Nitzschia palea* (Kütz.) W.Sm. 1853
NitzPerm	*Nitzschia perminuta* (Grun.) M. Perag. 1903
NitzRec	*Nitzschia recta* Hantzsch ex Rabenh. 1861
NitzSinT	*Nitzschia sinuata* var. *tabellaria* (Grun.) Grun. ex. Van Heurck 1885
RhAbbrev	*Rhoicosphenia abbreviata* (Ag.) Lange-Bertalot 1980
StCfAgas*	*Stephanodiscus* cf. *agassizensis* Håkansson & Kling sp.nov. 1989
StAlp*	*Stephanodiscus alpinus* Hustedt in Huber-Pestalozzi
StHantz*	*Stephanodiscus hantzschii* Grun. in Cleve & Grun. 1880
StHantzT*	*Stephanodiscus hantzschii* fo. *tenuis* (Hust.) Håkansson & Stoermer stat nov. 1984
StNeo*	*Stephanodiscus neoastraea* Håkansson & Hickel 1986
StParvus*	*Stephanodiscus parvus* Stoermer & Håkansson 1984
SurBreb	*Surirella brebissonii* Krammer & Lange-Bertalot 1987
SurMin	*Surirella minuta* Breb. ex Kutz. 1849
SynAcA*	*Synedra acus* var. *angustissima* (Grun. in van Heurck) van Heurck 1885
SynAcR*	*Synedra acus* var. *radians* (Kütz.) Hust. 1930
SynRump*	*Synedra rumpens* Kütz. 1844
SynRuFa*	*Synedra rumpens* var. *familiaris* (Kütz.) Hust. 1930
SynRuFr*	*Synedra rumpens* var. *fragilarioides* Grun. in Van Heurck 1881
SynRuSc*	*Synedra rumpens* var. *scotica* Grun. in Van Heurck 1881
TabFloc*	*Tabellaria flocculosa* (Roth) Kütz. 1844
ThalBram*	*Thalassiosira bramaputrae* (Ehrenb.) Håkansson & Locker 1981
AulAlpg	*Aulacoseira alpigena* (Grunow) Krammer 1990
CycCom	*Cyclotella comensis* Grun. in Van Heurck 1882
CycKram	*Cyclotella krammeri* Håkansson 1990
SynTen	*Synedra tenera* W. Sm. 1856

APPENDIX FOUR

Biovolume measurements of all diatom taxa included in biovolume calculations in Chapters 6 and 8

Full name	Biovolume µm³	Source	Full name	Biovolume µm³	Source
Achnanthes lanceolata	138	c	*Fragilaria capucina var. distans*	116	c
Achnanthes minutissima	55	c	*Fragilaria capucina var. gracilis*	100	b
Achnanthes oblongella	200	b	*Fragilaria capucina var. mesolepta*	340	c
Achnanthes pusilla	78	c	*Fragilaria capucina var. rumpens*	119	c
Actinocyclus normanii fo. *subsalsa*	5429	a	*Fragilaria crotonensis*	358	c
Amphora inariensis	150	b	*Fragilaria elliptica*	100	b
Amphora libyca	1473	c	*Fragilaria fasciculata*	234	c
Amphora montana	215	c	*Fragilaria parasitica*	139	c
Amphora ovalis	1000	b	*Fragilaria pinnata*	111	c
Amphora pediculus	98	c	*Fragilaria vaucheriae*	217	c
Amphora veneta	581	c	*Frustulia vulgaris*	1000	b
Asterionella formosa	496	c	*Gomphonema angustatum*	846	c
Aulacoseira ambigua	618	a	*Gomphonema clavatum*	1000	b
Aulacoseira granulata	1430	a	*Gomphonema minutum*	302	c
Aulacoseira granulata var. *angustissima*	302	a	*Gomphonema olivaceum*	391	c
Aulacoseira islandica	2714	a	*Gomphonema olivaceum* var. *minutissimum*	160	c
Aulacoseira subarctica	302	a	*Gomphonema parvulum*	218	c
Aulacoseira subarctica fo. subborealis	174	a	*Gomphonema truncatum*	1242	b
Caloneis amphisbaena	2500	b	*Gyrosigma accuminatum*	7021	c
Cocconeis pediculus	3114	c	*Hantzschia amphioxys*	1045	c
Cocconeis placentula	756	c	*Melosira varians*	5207	c
Ctenophora pulchella	1862	c	*Meridion circulare*	635	c
Cyclostephanos dubius	523	a	*Navicula (Sellaphora) bacillum*	800	b
Cyclostephanos invisitatus	201	a	*Navicula atomus*	40	b
Cyclostephanos tholiformis	65	a	*Navicula capitata*	623	c
Cyclotella atomus	65	a	*Navicula capitata* var. *hungarica*	187	c
Cyclotella meneghiniana	1078	a	*Navicula capitatoradiata*	449	c
Cyclotella meneghiniana (BBK surface sed)	5429	a	*Navicula cari*	141	c
Cyclotella ocellata	190	c	*Navicula cincta*	400	b
Cyclotella pseudostelligera	50	a	*Navicula clementis*	800	b
Cyclotella radiosa	2105	a	*Navicula cocconeiformis*	1235	b
Cymatopleura solea	6098	c	*Navicula cryptocephala*	340	c
Cymbella affinis	516	c	*Navicula cryptocephala / menisculus*	289	b
Cymbella amphicephala	500	b	*Navicula cryptotenella*	228	c
Cymbella cymbiformis	834	c	*Navicula cuspidata*	4000	b
Cymbella microcephala	59	a	*Navicula expecta*	400	b
Denticula kuetzingii	250	b	*Navicula gregaria*	230	c
Diatoma mesodon	935	c	*Navicula lanceolata*	1259	c
Diatoma tenuis var. *elongatum*	284	c	*Navicula menisculus*	350	c
Diatoma vulgaris	3786	c	*Navicula perminuta*	72	c
Diploneis parma	292	b	*Navicula phyllepta*	400	b
Encyonema caespitosum	1000	b	*Navicula pseudolanceolata*	1259	c
Encyonema minutum	250	b	*Navicula pupula*	621	c
Encyonema silesiacum	505	b	*Navicula pygmaea*	500	b
Eunotia bilunaris	759	b	*Navicula radiosa*	1110	c
Eunotia minor	638	b	*Navicula rhynchocephala*	716	c
Eunotia spp.	700	b	*Navicula salinarum*	887	c
Fragilaria brevistriata	146	c	*Navicula slesvicensis*	800	b

Full name	Biovolume μm^3	Source	Full name	Biovolume μm^3	Source
Navicula spp.	525	b	*Pinnularia microstauron*	1750	b
Navicula striolata	1500	b	*Pinnularia subcapitata*	766	c
Navicula tripunctata	926	c	*Rhoicosphenia abbreviata*	510	c
Navicula trivialis	977	c	*Stauroneis acuta*	10000	b
Navicula veneta	154	c	*Stauroneis smithii*	556	b
Neidium binodis	450	b	*Stephanodiscus alpinus*	1325	a
Nitzschia acicularis	187	c	*Stephanodiscus* cf. *agassizensis*	2104	a
Nitzschia amphibia	188	c	*Stephanodiscus hantzschii*	1608	a
Nitzschia angustata	5260	c	*Stephanodiscus hantzschii* fo. *tenuis*	4181	a
Nitzschia bacillum	91	c	*Stephanodiscus minutulus*	179	c
Nitzschia capitellata	395	c	*Stephanodiscus neoastraea*	16837	a
Nitzschia dissipata	258	c	*Stephanodiscus parvus*	108	a
Nitzschia fonticola	103	c	*Surirella angusta*	1128	c
Nitzschia frustulum	51	c	*Surirella bifrons*	20000	b
Nitzschia gracilis	399	c	*Surirella brebissonii*	1299	c
Nitzschia hungarica	884	c	*Surirella elegans*	52916	b
Nitzschia linearis	2871	c	*Surirella minuta*	984	c
Nitzschia monachorum	2000	b	*Surirella robusta*	20000	b
Nitzschia palea	281	c	*Synedra acus*	1420	c
Nitzschia paleacea	93	c	*Synedra acus* var. *angustissima*	1008	c
Nitzschia pellucida	500	b	*Synedra acus* var. *radians*	1448	c
Nitzschia pura	228	b	*Synedra nana*	100	a
Nitzschia recta	1571	c	*Synedra rumpens*	119	c
Nitzschia sinuata var. *delognei*	578	c	*Synedra rumpens* var. *familiaris*	181	c
Nitzschia sinuata var. *tabellaria*	260	c	*Synedra ulna*	6196	c
Nitzschia spp.	115	b	*Tabellaria flocculosa*	344	c
Nitzschia subacicularis	153	b	*Thalassiosira bramaputrae*	3637	a
Nitzschia vermicularis	484	a	*Thalassiosira pseudonana*	25	a
Pinnularia interrupta	1500	b	*Tryblionella levidensis*	1767	c

Source codes **a**, **b**, **c**, refer to the methods used to calculate biovolumes of individual taxa:

a: Biovolumes calculated using cell dimensions measured under both LM and SEM in this study, entered into the program BIOVOL (Kirschtel, 1996) and calculated using formulae specific to the shapes of individual diatom taxa. In the absence of reliable height estimates, centric diatom cell volumes were estimated using the assumption that the height of each cell was approximately half it diameter (cf. Bailey-Watts *et al.*, 1989). The unmeasured heights of pennate taxa were assumed to be equal to their minor semi-axis length.

b: Biovolumes calculated using average published cell dimensions (Krammer and Lange-Bertalot, 1986, 1988, 1991a, 1991b or Cox, 1996), entered into the program BIOVOL (Kirschtel, 1996) and calculated using formulae specific to the shapes of individual diatom taxa.

c: Biovolumes of individual diatom taxa taken directly from The Academy of Natural Sciences (2001) list of biovolumes. Occasionally assumptions have been made concerning harmonisation of individual taxon names in this study with those in the list.

APPENDIX FIVE

Diatom taxonomy – Aulacoseira spp. from UK lowland reservoirs

Taxa of the genus *Aulacoseira* Thwaites, are frequently found to be a major component of freshwater phytoplankton communities (e.g. Siver & Kling 1997; Reynolds & Irish, 2000; Haworth, 1988). However, some *Aulacoseira* taxa are morphologically similar when viewed in either girdle or valve views alone through the LM, particularly since individual taxa can themselves exhibit considerable morphological variation, leading to taxonomic confusion. Hustedt (1930) noted the highly polymorphic nature of valve structure in many *Aulacoseira* species. In common with other researchers, difficulties were often encountered in the identification and quantification of *Aulacoseira* species in the current study. Critical examination of selected samples under the scanning electron microscope (SEM) has helped to define distinguishing characteristics, assisting in the analysis of material routinely observed using the light microscope (LM) alone. What follows is a synopsis of the full spectrum of *Aulacoseira* species found in the plankton, surface sediments and core material of UK lowland reservoirs. Any difficulties encountered in making taxonomic distinctions are discussed.

Notes

- All LM pictures are of relative size, but a scale bar is provided for ease of comparison.
- All SEM pictures have their own scale.
- Areolae (pores) are holes in the valve face or mantle
- RP is an acronym for 'rimoportulae'
- Pseudoseptum (or 'Ringleiste) is the term used to describe the solid circular ridge or ledge of silica projecting inwards from near the margin of the mantle.
- Sulcus is the term used to describe the inward fold of the silica cell wall that occurs in a few species of *Aulacoseira* e.g. *A. ambigua*
- Separating spines are spines that link together valves from the same cell
- Linking spines are spines that link cells from different valves

Aulacoseira granulata (Ehrenberg) Simonsen 1979

Aulacoseira granulata was the most common and widespread *Aulacoseira* species of UK lowland reservoirs. It was present in the surface sediments of 23 training set sites (mean % relative abundance of 4.3%), being particularly well represented in Thornton (42.2%), Ardleigh (25.4%), Blagdon (19.9%), Swithland (13.5%), Chew (12.8%) and Porth (11.7%). *A. granulata* was also dominant in the late summer / autumn phytoplankton of a number of reservoirs, most prominently in Chew and Blagdon. In common with Siver & Kling (1997), small specimens of *A. granulata* were sometimes hard to separate from those of *Aulacoseira ambigua*, especially in the absence of separating spines. However, the ensuing discussion aims to highlight key features that usually enabled delineation of these species in this study.

The size range of *A. granulata* was considerable, the mantle height to valve diameter ratio ranging from 0.9 to 3. Siver and Kling (1997) reported ratios between 1.5 and ~3.3 from Connecticut lakes and prairie lakes and rivers in Canada. The lower ratios for valves in the UK lowland reservoir training set were attributable to some particularly large, square extremely coarsely areolated examples found in the plankton and surface sediments of Chew, Blagdon and Blackbrook reservoirs.

The areolae on the mantle of *A. granulata* are large, coarse and most often square in outline. They are straight on separating valves (Plate 1b,i) but curved on linking valves (Plate 1a,c,d,g), yielding a distinct dimorphic character. *A. granulata* differs from *A. ambigua* in its larger, coarser areolae, which are usually less 'neatly' arranged than in *A. ambigua*. Another feature useful for distinguishing between *A. granulata* and *A. ambigua* is the location of the RP. This cannot always be seen under either LM or SEM since its visibility is dependent upon valve orientation. However, on those valves where it can be distinguished, it is situated close to the second or third row or areolae from the collum (Plate 1g,j). In *A. ambigua* it is located just above the collum (Plate 3m,n,r). Both separating and linking spines were present, although separation valves were seen less frequently. Linking spines were similar in morphology to those of *Aulacoseira ambigua* (see below). Separating spines were sharply pointed, varying in length on individual specimens and between valves. Where present, these enabled a straightforward distinction between *A. granulata* and *A. ambigua*, but where absent further features (see above) required examination. Siver & Kling (1997) note a smooth valve face, however the nature of the valve faces in this study cannot be confirmed since no valve faces were located during SEM analyses.

Aulacoseira granulata var. _angustissima_ (O.Müller) Simonsen 1979, and _Aulacoseira granulata_ var. _angustissima_ f. _curvata_ (O.Müller) Simonsen 1979

Aulacoseira granulata var. *angustissima* was a fairly common planktonic diatom, being present in the surface sediments of 19 reservoirs. In 10 of these water bodies *A. granulata* var. *angustissima* was found in combination with the nominate *A. granulata*. However in all cases only the nominate or the variety was dominant in the relationship, co-dominance was never encountered. *A. granulata* var. *angustissima* was only found as a highly significant component in the surface sediments of two reservoirs – Grafham (26.5%) and Staunton Harold (27.2%) and occurred as a single species seasonal bloom in the plankton of Hawkridge reservoir in May 1999.

A. granulata var. *angustissima* is delineated from the nominate by the longer, thinner valve morphology and finer punctae. Valve dimensions of *A. granulata* var. *angustissima* in the current study were in the range 12-17 μm long by 3-4.5 μm wide. As in the nominate, both separating and linking spines were present, both possessing a similar morphology to those of *A. granulata*. The RP was in the same position as in *A. granulata* and in common with the nominate, was a useful feature for delineation from *A. ambigua*. Further features enabled *A. granulata* var. *angustissima* to be relatively easy to separate from *A. ambigua*: Firstly, the areolae, despite being generally smaller and finer than those in *A. granulata*, were never quite as small or so neatly arranged as in *A. ambigua*. Secondly, due to the narrow nature of the valves, the areolae usually appeared to be arranged in irregular straight rows as opposed to the spiralling rows seen in *A. ambigua*. Thirdly, the cell walls were usually very thin and straight with distinctive bulges at the juncture of valves, distinguishing them from *A. ambigua* that has slightly thicker cell walls and a hollow sulcus (see below).

The only difference between *A. granulata* var. *angustissima* and *A. granulata* var. *angustissima* fo. *curvata* is the curved nature of both individual valves and chains of valves. *A. granulata* var. *angustissima* fo. *curvata* was only found in the plankton and surface sediments of two reservoirs. In Daventry it made up 2.6% of the surface sediment assemblage and in Weir Wood its relative abundance was 2.7%. In both reservoirs *A. granulata* var. *angustissima* fo. *curvata* was found in association with *A. granulata* var. *angustissima* and alongside a small percentage of the nominate, *A. granulata*. Counts of *A. granulata* var. *angustissima* fo. *curvata* were recorded separately to enable assessment of the ecological significance of occurrence of this particular morphotype.

***Aulacoseira ambigua* (Grun. in Van Heurck) Simonsen 1979**

Aulacoseira ambigua was a commonly occurring planktonic diatom species, being found in the surface sediments of 21 sites in the data set, with relative frequencies in the range 0.2% to 42.0% (mean 4.8% for all sites). Sites with the greatest relative frequencies were Darwell (42.0%), Hollowell (37.6%), Wimbleball (36.8%), Upper Tamar (21.0%), Clatworthy (20.3%), Chelmarsh (17.7%) and Arlington (13.8%).

Cells of *A. ambigua* consisted of valves that were longer than wide, possessing spiralling pervalvar rows of mantle areolae and having a relatively plain valve face (rarely seen). The height of the valve mantle was most often 2 to 2.3 times the diameter of the valve (range 1.1 to 3.9). There was generally less variation in *A. ambigua*'s valve morphology than that observed for *A. granulata* (see above) and *Aulacoseira subarctica* (see below). Morphology was surprisingly similar in the majority of reservoirs where *A. ambigua* occurred, however in Wimbleball valves were consistently long and thin (3.9:1) and in Chelmarsh they were almost square (1.1:1). Pervalvar rows of areolae alternated with costae; each costae terminated at a spine. The mean number of areolae and pervalvar rows of areolae in 10μm was 18 (range 16-20). The above observations compared well with those noted by Siver & Kling (1997), who recorded mantle height to diameter ratios of 1.5:1 to 3:1, with a mean of 18 rows of pervalvar areolae in 10μm.

A. ambigua cells were rarely found individually, instead they were usually found in pairs or long chains. Since the linking spines are triangular and tightly interlocking, it was less common to see separation at the linking spines and therefore more common to see cells from different valves joined together in pairs by the linking spines. This is in stark contrast to *A. subarctica*, where cells usually remain intact (see below). In *A. ambigua* the RP is located just above the collum (Plate 3m,n,r), differing in its position to that seen in *A. granulata* (Plate 1g,j)

Siver & Kling (1997) observed that a thin membrane often covered the mantle areolae, and that as the cell aged the remains of the membrane degraded and revealed the areolae. A similar obscuration, or occlusion of the areolae occurred in this study (see Plate 3r).

Aulacoseira islandica (O. Müller 1906) Simonsen 1979

Aulacoseira islandica is a widely distributed freshwater diatom, frequently dominant or subdominant in cold-season plankton assemblages, particularly in large lakes (Lund 1962, Stoermer *et al.* 1981, Genkal & Popovskaya 1991, Siver & Kling 1997). *A.islandica* only occurred in 4 UK lowland reservoirs, all located in the Leicestershire region – Blackbrook, Cropston, Nanpantan and Swithland. In these reservoirs *A.islandica* was most dominant in Swithland, both in the plankton (virtually single species bloom colouring the water brown in March 2000) and in the surface sediment (31.4% relative abundance). In Blackbrook, Cropston and Nanpantan its contribution to the surface sediment diatom flora was less pronounced, with relative abundances of 5.8%, 6.1% and 4.4% respectively.

Le Cohu (1996) made detailed observations on the fine structure of *A.islandica*. He noted the presence of separation relief valves with a stepped mantle and tapering spines (Plate 4l), whereas despite commonly possessing a stepped mantle, linking valves always had spathulate spines firmly interlocking the sibling valves (Plate 4j,k,m). He also noted that the presence of several RP on the mantle was one of the most striking features in *A.islandica*. These RP can be seen particularly clearly under the LM as 'halos' around the areolae (Plate 4a,d,f,g). *A.islandica*'s valve face is areolate (Plate 4n).

A.islandica was usually easy to distinguish from *A. granulata* and *A. ambigua* due to its straight, regular rows of pervalvar areolae and overall squarer valve proportions. However in some instances, particularly in the recent sediments of the long core BBK00C, longer, narrower morphs were encountered which presented identification problems.

In addition, they observe that cell volume becomes larger in intense light. It was noted in the long core BBK00C, that the size and structure of valves became finer over time. In the surface sediments in particular, valves were often found to be longer, narrower and more delicate than at depth (Plate 4m,n), occasionally resulting in taxonomic confusion with *A. ambigua*. Stoermer *et al.* (1985) distinguished three morphotypes of *A.islandica* preserved in the sediments of Lake Ontario (Canada). They noted that the morphological variations encountered were related to silicon availability. Coarse-structured specimens occurred when silica was available in excess and fine-structured forms were present when phosphorus loading increased and silica thus depleted due to enhanced diatom production. Brown & Richardson (1968) in Willén (1991) supply an alternative or perhaps complimentary view. They relate pore size to light climate, proposing that large-pored forms dominate during

periods of deep mixing (low light) and small-pored forms prevail when the water column is more stable (increased light).

Aulacoseira subarctica (O. Müller 1906) Haworth 1988

This taxon is well known from phytoplankton studies (e.g. Lund 1954, 1955, 1979; Haworth 1988; Siver & Kling 1997). According to Haworth (1988), typically chains consist of frustules where the valves are c. 6-10μm in diameter and 7-10μm high. The valves always have long pointed, equal-sized spines that are rather thick at the base. These are visible both at the ends of the filaments and often overlying the adjacent cells (see Plate 5r,t,u). They are arranged regularly around the valve margin alternating with external grooves that accommodate the spines of the sibling valve; this is easily seen under the LM. This arrangement allows the cells to slide apart freely, resulting in the frequent occurrence of pairs of valves (1 cell) (e.g. Plate 5g,j,n), or chains of four valves (2 cells) (e.g. Plate 5b,c,d,e,h,u) where girdle bands are visible overlying newly formed sibling valves (see Plate 5u and compare with Fig.10 in Canter & Haworth (1991)). In common with Siver & Kling (1997), only separating spines were observed for *A. subarctica*. Conversely, *A. ambigua* possesses triangular linking spines with crescentic edges and small, regularly pointed separation spines (see discussion above).

In *A. subarctica*, fine pores are arranged in regular rows (15-20 /10 μm); the rows curve along the valve mantle, and line up with both the spines and grooves. The valve face may be plain or may more commonly have fine pores positioned on the valve periphery each in line with and positioned adjacent to a spine (see Plate 5r,s). The silica cell walls are thicker than those of *A. ambigua*, *A. granulata* and *A.islandica*, especially the thickened area of the pseudoseptum, which is visible in both girdle and valve views, under LM. Viewed under SEM, the pseudoseptum was thick and solid in all specimens and usually extended inward about one quarter to one half of the radius (Plate 5t). In common with Siver and Kling (1997), this distance was closely related to the mantle height to valve diameter ratio.

In UK lowland reservoirs, *A. subarctica* exhibited a wide range of valve morphologies, as can be seen from Plate 5. The mantle height to valve diameter ratios ranged from 0.5 to 2.9. The longer, narrower valves characteristic of sites such as Porth (Plate 5q), Leigh (Plate 5e), Wistlandpound (Plate 5m,n) and occasionally Blackbrook (Plate 5g) (see below) had valves with heights of 8-13 μm and diameters of 4.5-5.5 μm, resulting in ratios of 1.7-2.8. In

contrast, other examples were square in appearance e.g. samples from Bewl (Plate 5b,c), Powdermill (Plate 5a) and Durleigh (5d), generating ratios of around 1:1. At the other end of the spectrum, specimens were encountered which were squatter in appearance e.g. from Trimpley (Plate 5j,k) and Blackbrook (Plate 5h,u), resulting in ratios of between 0.5 and 1. In all cases there were between 15-18 pervalvar rows of areolae per 10μm, conforming with the number described by Haworth (1988) and the mean of 18 presented by Siver and Kling (1997).

It was common for plankton samples to contain 'blooms' where particular valve morphologies dominated. For example, Porth reservoir produced a huge population of the long, narrow form of *A. subarctica* in the phytoplankton in March 2000 (Plate 5p,q). Although some chains of more squat forms were present (Plate 5p), the bloom was largely of this single morphological type. Jewson (1992) found a wide range in the diameters of valves in Lough Neagh, Northern Ireland, but noted that over 90% of frustules were within a small range in valve diameter because of processes that preferentially removed both narrow and broad valves. Thus, differing morphologies of *A. subarctica* valves may reflect environmental characteristics and may therefore afford useful ecological information. However, in the current study, *A. subarctica* has only been distinguished from *A. subarctica* fo. *subborealis*.

***Aulacoseira subarctica* (O. Müller 1906) Haworth 1988 fo. *subborealis* (Nygaard 1956) Haworth 1988**

Aulacoseira subborealis stat. nov (Denys *et al.*, 2003)

These specimens are somewhat smaller than the small form of *A. subarctica*, but it is still unsure whether *A. subarctica* fo. *subborealis* is just an extreme variation of the nominate (Haworth, 1988), or whether it is a species in its own right (Denys *et al.*, 2003). Although the valves are smaller, the basic pattern of mantle striae related to both spine and groove remains constant. The spines were not as long and thus the characteristic 'tongue and groove' system of overlap seen in *A. subarctica* was less apparent. In addition, the linking spines are smaller and non-spathulate and do not have areolae at their base (Denys *et al.*, 2003), unlike the nominate. Haworth (1988) states that 'it remains possible that this form may represent part of a continuum, rather than a separate entity'. However, Haworth (1988) also suggests that the presence of these squat forms may be of ecological significance and their distinction is worthy of note. Thus *A. subarctica* fo. *subborealis* has been distinguished

from the nominate in this study. It is possible that *A. subarctica* fo. *subborealis* may have previously been misreported as *A. distans* or *A. alpigena* in a number of studies due to superficial similarities, however mantle areolation is coarser in these taxa (Denys *et al.*, 2003).

A. subarctica fo. *subborealis* was only found in the surface sediments and plankton of 2 reservoirs – Sutton Bingham and Durleigh. These reservoirs are alkaline, relatively shallow, turbid and eutrophic. The occurrence of *A. subarctica* fo. *subborealis* in these environments supports observations made by Tibby (2004) from material from SE Australian billabongs and reservoirs in the same region. Denys *et al.* (2003) report that *A. subarctica* fo. *subborealis* is typical of turbid environments.

In both Sutton Bingham and Durleigh the morphology of *A. subarctica* fo. *subborealis* was constant, comprising valves of between 5 - 6.4 μm in diameter and 2.8 – 3.9 μm in height (Plates 6a,b,c,e,g,h) (c.5 μm by 3 μm reported by Haworth (1988) for samples from Michigan and New Zealand lakes), with 24-26 mantle areolae in 10 μm (contrasting with 15-18 for *A. subarctica* (this study) and 15-24 for *A. alpigena* (Haworth (1988)). The height to diameter ratio was always close to 0.5, contrasting with the large range seen in *A. subarctica* (0.5 - 2.8) and is therefore another useful distinguishing feature between the two forms when combined with the other features discussed above. Finally, all examples viewed under SEM were seen to possess perforated disci (Plate 6d,e,f), unlike *A. subarctica* where valve faces were usually plain, with areolae only present around the margins (Plate 5).

***Aulacoseira alpigena* (Grunow) Krammer**

Aulacoseira distans var. *alpigena* (Grunow) Simonsen

Aulacoseira lirata var. *alpigena* (Grunow) Haworth

Found only in Trenchford reservoir, this species was initially thought to be *A. subarctica* fo. *subborealis* because of their similar dimensions and appearance under LM. However, a few subtle morphological differences along with knowledge of the contrasting environmental conditions between Trenchford and Sutton Bingham / Durleigh (*A. subarctica* fo. *subborealis* sites) raised suspicions as to the identity of this small *Aulacoseira* taxon.

When viewed under the SEM it became apparent that the small *Aulacoseira* species did not fit the description of *A. subarctica* fo. *subborealis*, but was instead much more similar to the

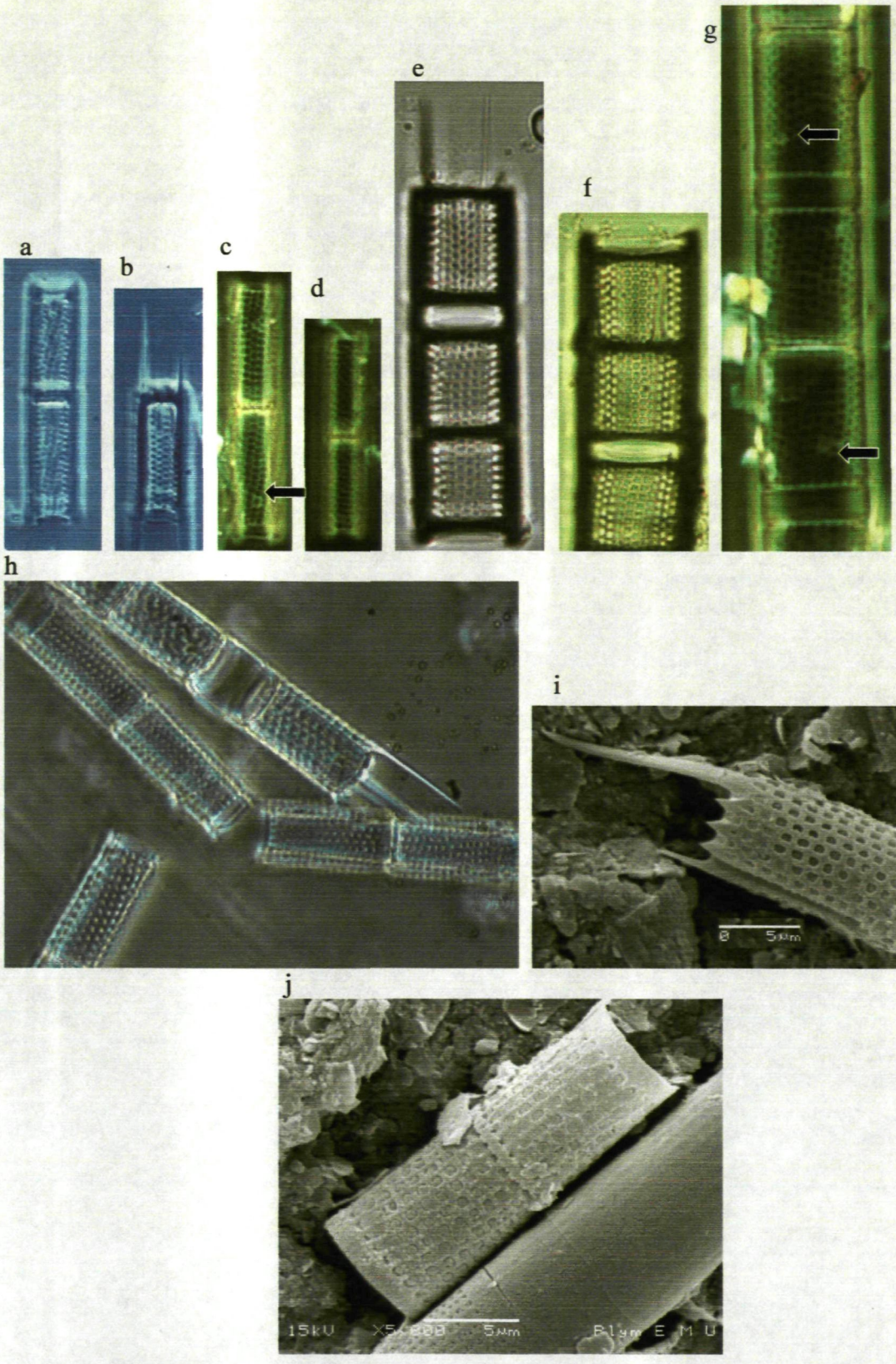
features of *Aulacoseira alpigena*. The ecology of this species complemented the site characteristics of Trenchford reservoir, unlike that of *A. subarctica* fo. *subborealis*.

Straie on the mantle usually alternated with the marginal spines. Haworth (1988) describes the marginal spines of *A. alpigena* as varying between small and pointed to larger and irregularly spathulate; the former type separating readily but those with the latter type being firmly interlocked and thus nearly always found as sibling valves and rarely seen in valve view. This fits observations in the current study. Individual valves were rarely seen in valve view under the SEM or LM.

Haworth (1988) and Krammer and Lange-Bertalot (1991) describe *A. alpigena* as having a wide range in the number of areolae per pervalvar straie (4 to 15), positioned in curved rows (*A. lirata* has 5 or 6 (Haworth (1988)). The specimens in this study had between 5 and 8 areolae in a pervalvar straie (most had 8) and the rows were usually slightly oblique, although ranged from straight in the squatter examples to curved in the larger specimens. Krammer (1991a) describes *A. alpigena* as having linking spines that are spatulate in shape with lateral projections. Trenchford's specimens were found to possess both spatulate and shallow cruciform-shaped linking spines.

Haworth (1988) describes *A. alpigena* as being 4-11 μm wide and 3-6 μm deep with 15-24 mantle straie in 10μm. The examples below range from 7-14 μm wide and 3-6 μm deep and all have ~15 straie in 10μm. Although Trenchford's specimens were often slightly wider than Haworth's (1988) description and the number of mantle straie was at the low end of her range, it was decided that for both this feature and the characteristics described above, *A. alpigena* best described this specimen.

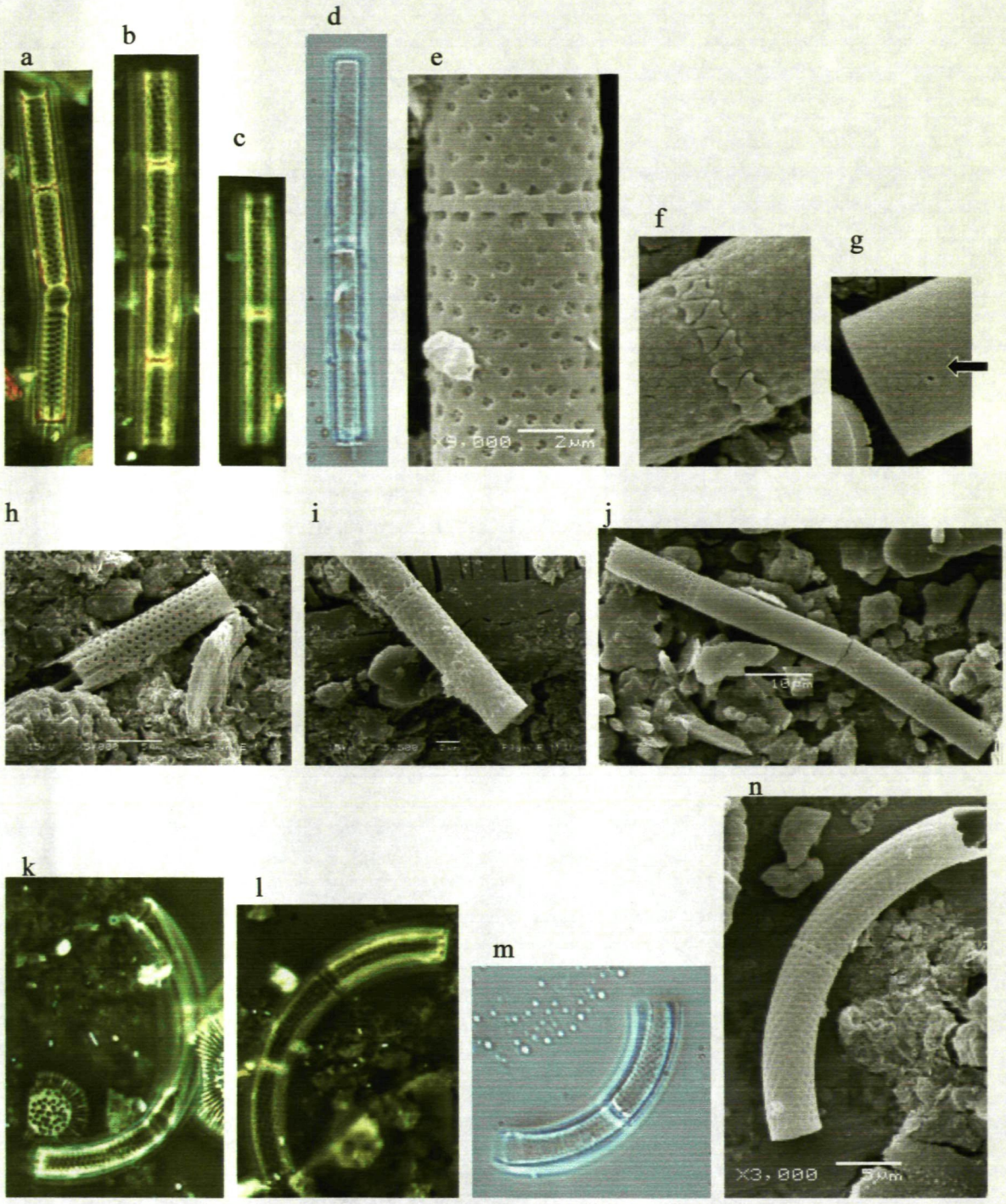
Siver & Kling (1997) and Haworth (1988) describe *A. alpigena* as occurring in waters of low alkalinity and nutrient concentrations and in waters where pH lies between 5 and 6 (Connecticut and Canadian Shield localities) and 6 and 7 (English Lake District). Trenchford seems to fit this ecological description, having a mean annual pH of 6.83, alkalinity of 7 mg Ca l^{-1} and conductivity of 106 (all the lowest values in the lowland reservoir training set), as well as extremely low concentrations of SRP and TP (4 and 11 μgl^{-1} annual averages respectively), but average concentrations of TON and TP (1.79 and 2.56 mgl^{-1} annual averages respectively).



——— = 10 µm for all LM images (SEM pictures have their own scales)

Plate 1 – *Aulacoseira granulata*

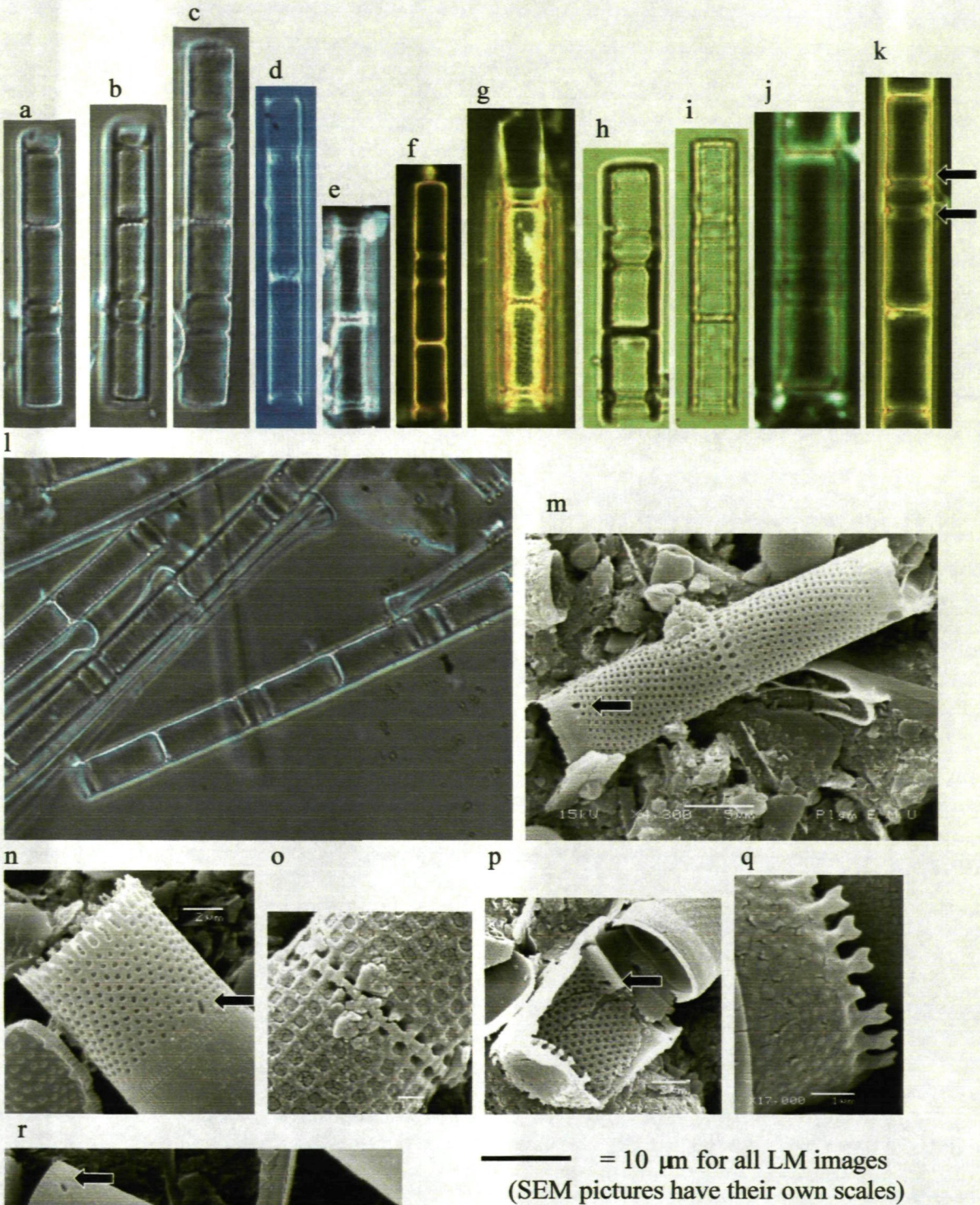
a) Porth PL (10/00); b) Porth PL (10/00) - separating valve - note the straight rows of areolae; **c) Thornton SS** – linking valves - note the curved lines of areolae - the location of the RP is arrowed and lies close to the 2nd/3rd row of areolae from the collum; **d) Swithland SS**; **e) Blackbrook 0-0.5cm** – large, square valves; **f) Chew PL (05/99)** – large square valves - linking valve at top with straight rows of areolae, those of the two separating valves below are curved; **g) BBK00C 4.5-5cm**, RP are arrowed and lie close to the 2nd/3rd row of areolae from the collum (compare with the RP location in *A. ambigua*, Plate 3 m,n,r); **h) Blagdon PL (10/00)**; **i) BBK00C 1-1.5cm** - separation spines; **j) BBK00C 1-1.5cm** - linking spines & coarse, square areolae.



——— = 10 μm for all LM images (SEM pictures have their own scales)

Plate 2 – *Aulacoseira granulata* var. *angustissima* (a-j)
***Aulacoseira granulata* var. *angustissima* fo. *curvata* (k-n)**

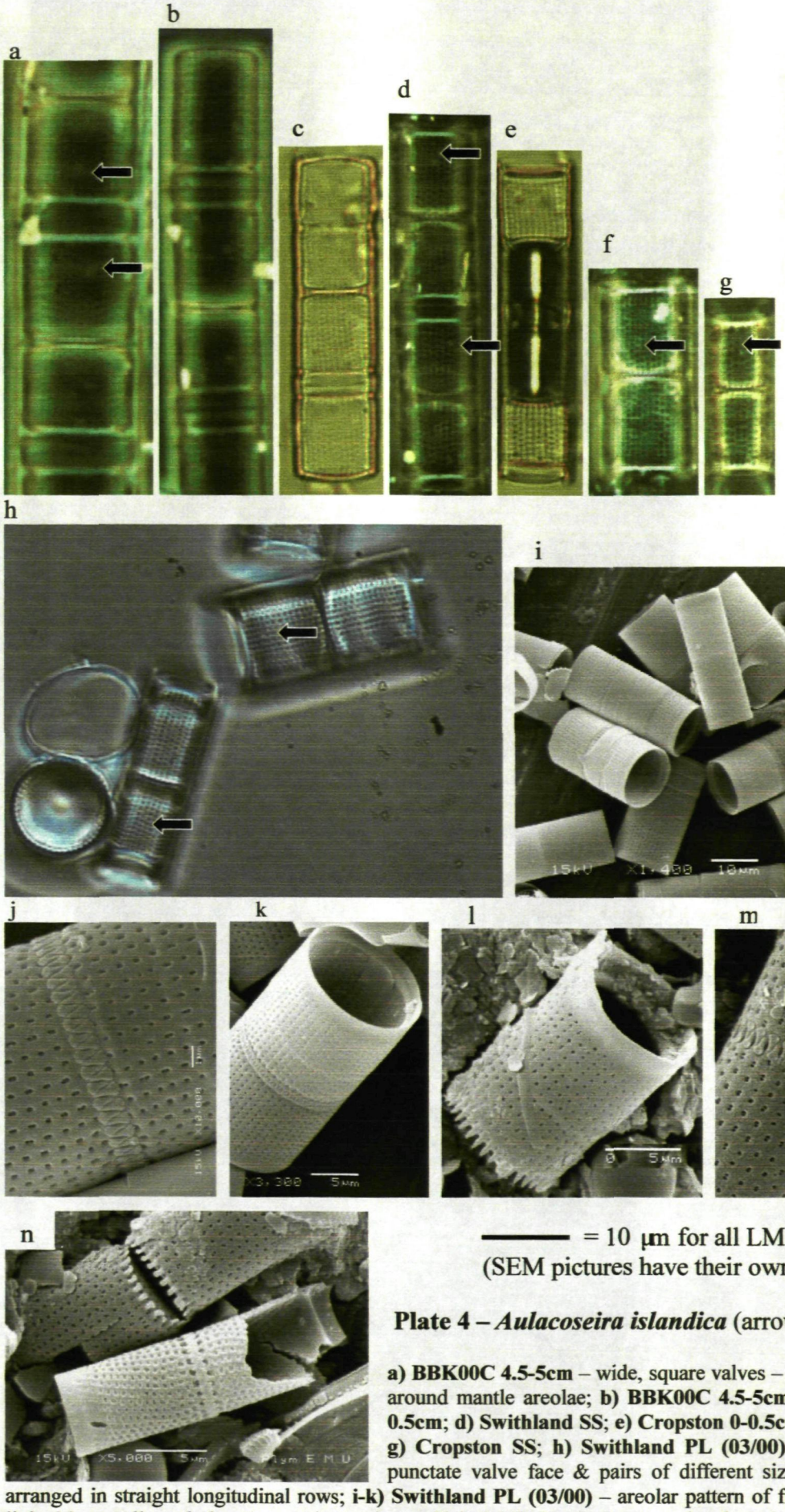
a) Weir Wood SS – note the narrow cells with thin cell walls and distinctive bulges at the juncture of valves (compare with the thicker cell walls and hollow 'sulcus' of *A. ambigua* in Plate 3); **b) Grafham SS**; **c) Tittesworth SS**; **d) Daventry PL (10/00)**; **e) Grafham SS** – linking valves with small, triangular, tightly interlocking linking spines and rather irregular areolae typical of the species; **f) BBK00C 18-19cm** - linking spines; **g) BBK00C 18-19cm** – note the similar RP position (arrowed) to that seen for *A. granulata*; **h) Daventry SS** - separation valve with straight rows of areolae and long separation spines (both features also seen in the nominate); **i) Daventry SS** - linking spines & collum; **j) Grafham SS**; **k) Weir Wood SS** – note the curved nature of the valves; **l) Daventry SS**; **m) Daventry PL (10/00)**; **n) Daventry SS** – note the slightly spiralling areolae on the linking valves, which are not as neat or as small as those of *A. ambigua* seen clearly in Plate 3m.



= 10 μm for all LM images
(SEM pictures have their own scales)

Plate 3 – *Aulacoseira ambigua*

a) Nanpantan PL (03/00) – note the 'eyes', which arise due to the hollow sulcus typical of *A. ambigua*; **b) Nanpantan PL (03/00)**; **c) Nanpantan PL (06/00)** – hollow 'sulcus'; **d) Wimbleball PL (10/00)**; **e) Wimbleball SS**; **f) Ogston SS** – note 'eyes'; **g) Clatworthy PL (03/00)**; **h) Blackbrook PL (05/99)**; **i) Blackbrook PL (07/99)**; **j) BBK00C**; **k) Luxhay SS** – note the hollow sulcus typical of this taxon; **l) Upper Tamar PL (03/00)**; **m) BBK00C 2-2.5cm** - linking spines and RP (arrowed); **n) Chelmarsh SS** – square linking valve - note the neat, spiralling areolae, the small triangular linking spines with crescentic edges and the position of the RP just above the collum; **o) BBK00C 1-1.5cm** - linking spines & quadrate areolae (areolae larger and more quadrate that those of *A. subarctica* in Plate 5, but smaller than those of *A. granulata* in Plate 1; **p) BBK00C 1-1.5cm** - internal view of broken valve, showing linking spines & the position of the RP adjoining the sulcus; **q) BBK00C 2-2.5cm** – detail of small triangular crescentic edged linking spines; **r) BBK00C 18-19cm** – note position of the RPs just above the collum - note the silica covering the areolae, which makes delineation of specimens of *A. ambigua* such as this very difficult under LM alone.



——— = 10 µm for all LM images
(SEM pictures have their own scales)

Plate 4 – *Aulacoseira islandica* (arrows indicate RPs)

a) BBK00C 4.5-5cm – wide, square valves – RPs show as 'halos' around mantle areolae; **b) BBK00C 4.5-5cm**; **c) Blackbrook 0-0.5cm**; **d) Swithland SS**; **e) Cropston 0-0.5cm**; **f) Swithland SS**; **g) Cropston SS**; **h) Swithland PL (03/00)** –bloom illustrating punctate valve face & pairs of different sized valves – areolae arranged in straight longitudinal rows; **i-k) Swithland PL (03/00)** – areolar pattern of fine pores – frustules linked by small spathulate (separating) spines which tightly interlock – note breakage by cell disruption and the presence of empty valves at the ends, sometimes terminated by the first girdle band (the valvocopula); **l) BBK00C 2-2.5cm** – end cell - note small triangular linking spines and straight rows of single areolae; **m) BBK00C 2-2.5cm** narrow valve; **n) BBK00C 2-2.5cm** – punctate valve face, spathulate separation spines & straight rows of single pores - compare overall appearance with that of *A. ambigua* pictured in the foreground.

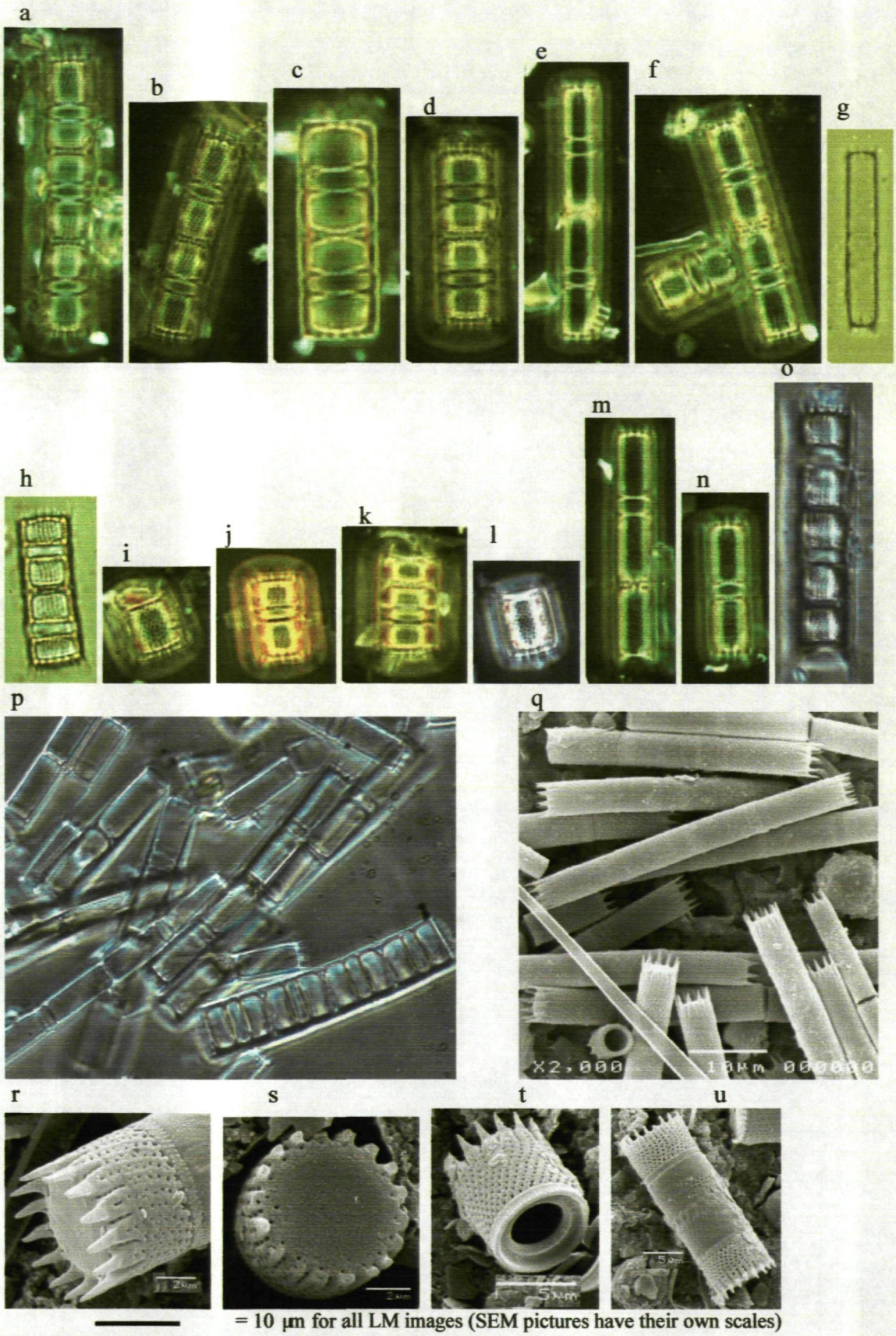
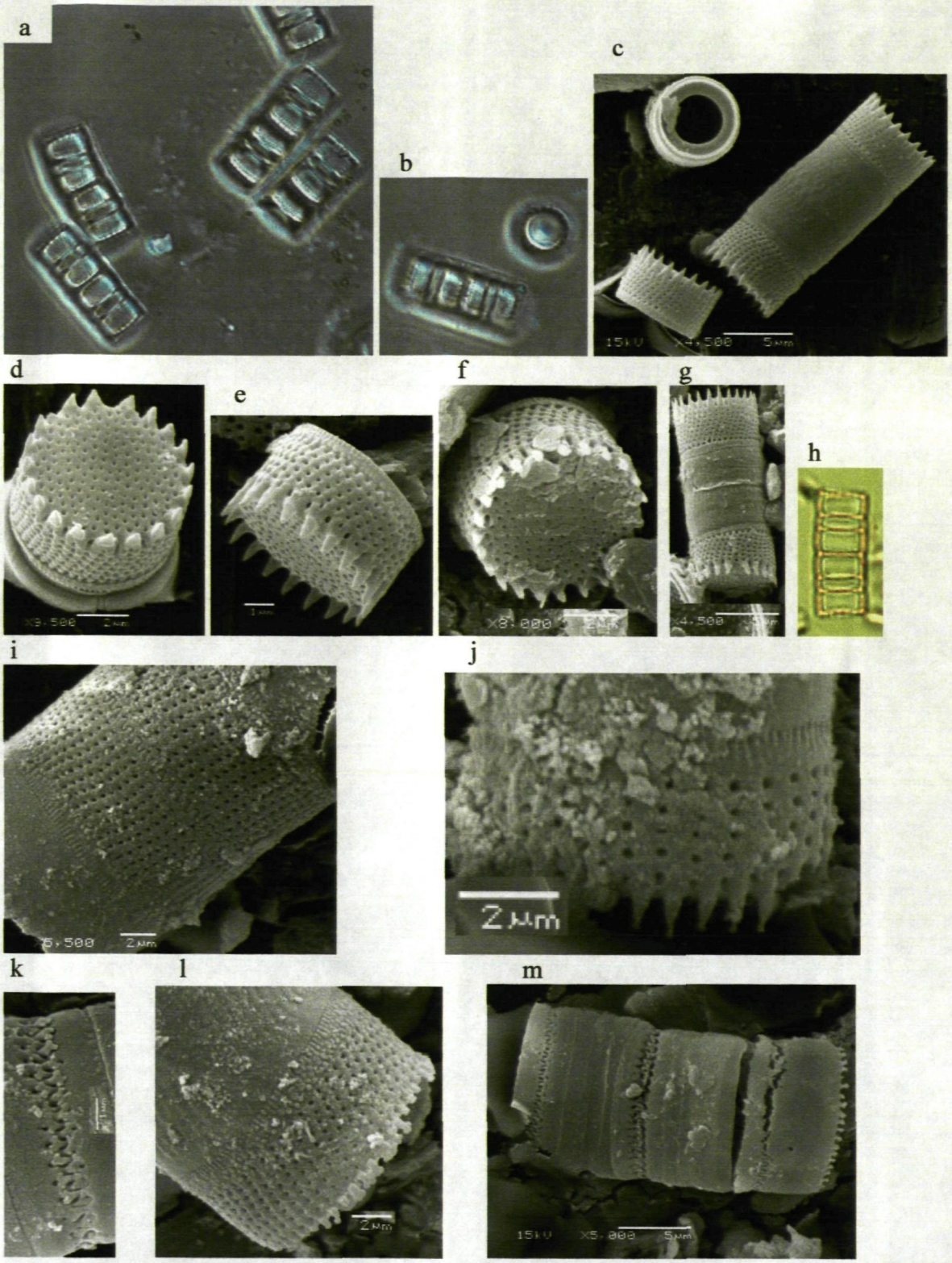


Plate 5 – Aulacoseira subarctica

a) Powdermill SS – note the thick cell walls, particularly the pseudoseptum (sulcus); **b-c) Bewl SS**; **d) Durleigh SS**; **e-f) Leigh SS**; **g-h) Blackbrook PL (07/00)**; **i) Tittesworth SS**; **j-k) Trimpley SS**; **l) Wimbleball SS** – note spiralling arrangement of fine mantle areolae; **m-n) Wistlandpound SS**; **o) Weir Wood PL (03/00)**; **p-q) Porth PL (03/00)** – note the predominance of long, thin valves, but (D=4.5µm, H=11µm), but also the presence of shorter, squatter valves; **r) BBK00C 18-19cm** – note ring of long, pointed, equal-sized spines and thus the ease with which cells can separate - lines of areolae end both at the base of spines and in the spine grooves; **s) BBK00C 18-19cm** - plain valve face with pores positioned at the periphery; **t) BBK00C 18-19cm** – note the wide pseudoseptum and spiralling arrangement of the fine mantle areolae; **u) BBK00C 2-2.5cm** – four squat valves - note the copulae visible overlying the newly-formed valves.



——— = 10 µm for all LM images (SEM pictures have their own scales)

Plate 6 –Aulacoseira subarctica fo. subborealis (a-h)
Aulacoseira alpigena (i-m)

a-b) Sutton Bingham PL (03/00) bloom; **c) Sutton Bingham PL (03/00)** – note the height to diameter ratio of ~0.5 (D=6.9µm x H=3.75µm); **d) Sutton Bingham PL (03/00)** - punctate valve face (note the plain valve face of the nominate in Plate 5r,s); **e) Sutton Bingham PL (03/00)** – note the shorter length of the linking spines than the nominate – note that there are no areolae at the base of the spines, unlike the nominate (Plate 5r); **f) Durleigh SS** - punctate valve face; **g) Durleigh SS**; **h) Durleigh 0-0.5cm**; **i-j) Trenchford SS** - separation spines and 1:1 spine to areolae ratio; **k) Trenchford SS** – linking spine detail; **l) Trenchford SS** - linking spine detail; **m) Trenchford SS** - linking spines and 1:1 ratio of spines to areolae.